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Seattle, Washington

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Fishery Bulletin

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EFFECTS OF OIL ON MARINE ECOSYSTEMS: A REVIEW FOR ADMINISTRATORS AND POLICY MAKERS

DALE R. EVANS[1] AND STANLEY D. RICE[2]

ABSTRACT

A broad selection of recent literature on the effects of oil on marine ecosystems is reviewed. The focus is on studies on crude oil, and the results are discussed with the purpose of providing a summary of findings that will be a useful reference for administrators and policy makers involved in decisions concerning petroleum developments and related activities. The characteristics of crude oil and factors modifying its impact on the marine environment are discussed. Most research on the toxicity of oil has dealt with acute effects and data on long-term impacts at the community level are inconclusive. It is concluded that chronic low-level pollution is potentially more damaging to ecosystems than isolated catastrophic spills. Decision makers are forced to rely on interpretative judgments rather than conclusive data.

Much of the material in this report was gathered as background material for use in preparing the marine section of the final environmental impact statement on the proposed trans-Alaska pipeline system (U.S. Department of the Interior, 1972). Some of the statements are essentially unchanged from the way they were presented in the appendix to volume IV of the impact statement. The impact statement made it clear that not enough data are available to analyze conclusively all of the potential environmental impacts of operation of the pipeline marine terminal facilities at Port Valdez, Alaska, and the transshipment of crude oil by tankers to west coast ports. A conclusion that can be drawn, however, and a message of the impact statement, is that oil poses a significant hazard to marine ecosystems, and a good deal of intensive research is necessary if these hazards are to be quantified and fully understood.

Research on oil pollution published since the impact statement on the pipeline was issued reveals that scant progress has been made, particularly with regard to the effects of chronic low-level oil pollution. Current and projected demands for energy in the United States are prompting accelerated development of offshore petroleum reserves, expanded oil tanker traffic, and proposals for construction of deepwater port facilities to handle the increasing number of supertankers. These developments will not wait for conclusive answers to questions on oil pollution. Recognizing this, we feel it is important that public administrators and policy makers be made aware of the inferences and trends evident in the research findings to date. These findings present a persuasive case that decisions regarding the handling of crude oil and petroleum products should be conservative and in favor of protecting the natural environment. While this report is by no means a complete review of the literature, it is sufficient to illustrate the potential danger of oil pollution to marine ecosystems and provide some guidance for policy decisions.

History is replete with examples of man's scientific and technological advances carrying him into situations he did not fully comprehend and with consequences he could not evaluate. Bella (1970) noted that "our ability to change this world is going to increase faster than our ability to predict what that change is going to be." He concludes that our management procedures must recognize the degree of ignorance we have about this world in which we live.

Pollution of the ocean by oil is a worldwide problem of growing concern to many nations. Spills like the *Torrey Canyon*, the *Arrow*, the Santa Barbara Channel blowout, and other spectacular incidents have helped stimulate international organizations of governments and industry to react to the problem. Viewed pragmatically, international response has been at least as adequate as domestic programs. Predicting the impact of an oil spill on the environment requires an understanding of the complex interactions involved. What

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appears to be universally lacking is the difficult research leading to an understanding of chronic and sublethal effects of oil at the biological community level. The following discussion outlines these complexities and points out how they make most generalizations invalid and the extrapolation of most data dangerous.

DESCRIPTION OF OIL

Crude oil is a complex mixture of many different specific hydrocarbons and a variety of compounds containing sulfur, oxygen, nitrogen, and some trace metals. Hydrocarbons make up the bulk of crude oil and can roughly be placed into one of three classes: paraffinic, naphthenic, and aromatic. From one area to another, crude oils vary in their composition and in density, volatility, and solubility. Their relative toxicity will vary (Ottway, 1971) but is roughly proportional to their aromatic content.

Paraffinic (or aliphatic) hydrocarbons are straight or branched carbon chains and are saturated (thus no carbon-carbon double bonds) with hydrogen or other groups. These hydrocarbons are the least toxic, although they may have an anesthetic or narcotic effect if concentrations are great enough.

Naphthenic compounds (cycloparaffins) contain at least one ring structure that is saturated. With this base, more rings or chains may be attached to form a variety of complex molecules.

Aromatic hydrocarbons also contain a ringed structure, but the ring is unsaturated with hydrogen and contains carbon-carbon double bonds (benzene ring). The simplest aromatic is benzene, which is very toxic and relatively water soluble in comparison to most hydrocarbons found in crude oil. Benzene and other low-boiling aromatics are the most toxic petroleum fractions. High-boiling aromatics act as slower poisons than low-boiling aromatics, but they are equally severe in their effect. In addition, some are known to induce cancer; 3,4-benzpyrene, 1,2-benzanthracene, and some alkylbenzanthracenes have been isolated from crude oil, and their carcinogenic effects on animals and man have been demonstrated (Blumer, 1970).[3]

Olefinic hydrocarbons (paraffinlike but unsaturated and containing reactive carbon-carbon double bonds) are not generally found in crude oils but are plentiful in certain gasolines and other refined products. The fate of olefins in the marine environment is poorly understood, but this class of compounds may be quite reactive under certain conditions and may combine readily with hydrogen, oxygen, chlorine, sulfur, and other elements to produce toxic substances. Once incorporated into organisms, olefins may remain intact for surprisingly long times (Blumer, 1967). The full range of olefinic hydrocarbons probably interferes with the reception of chemical messengers, or odors, in the sea by certain marine organisms (Blumer, 1970, see footnote 3).

When crude oil is processed ("cracked"), olefins and other compounds for gasoline and fuel oils may be formed or separated. Fuel oils, commonly involved in spills, are rated from 1 to 6. Those rated 1 are the lightest, most volatile, and most toxic and have the greatest aromatic concentrations; those rated 6 are the least volatile, least soluble, and least toxic and are asphaltic (tarlike).

Hydrocarbons are not foreign to the marine environment; normal paraffins are synthesized by most, if not all, living organisms. Blumer, Guillard, and Chase (1971) characterized the natural hydrocarbon content of 22 species of phytoplankton and cited literature for zooplankton. There are certain characteristic differences, however, between hydrocarbons native to organisms and the hydrocarbons in petroleum, particularly in the relative distribution of the various hydrocarbons. Crude oils and certain petroleum products are complex mixtures that contain molecules of different sizes in ratios not found in any one species of organism. Certain specific paraffins, and some naphthenic and aromatic compounds, are rarely found in organisms not exposed to oil pollution. These characteristic differences have been the basis for several scientific papers (Blumer, Souza, and Sass, 1970; Ehrhardt, 1972; Clark and Finley, 1973; and others).

FACTORS INFLUENCING THE IMPACT OF OIL

The impact of oil on the marine environment is governed by several factors—physical, chemical, and biological—in addition to the inherent complexity of crude oil and refined products. The behavior, effects, and fate of an oil spill involve all of

[3]Blumer, M. 1970. Scientific aspects of the oil spill problem. Presented at NATO Conference, Brussels, 6 Nov. 1970, 21 p., Woods Hole Oceanogr. Inst., Woods Hole, Mass.

these factors; and because they are interdependent, the reliability of our predictions concerning the impact of a spill is limited by our knowledge of the least understood variable.

Straughan (1972) noted our general inability to predict the environmental impact of a spill because of the complexity of the matter, and identified several factors that govern biological damage caused by a spill: 1) type of oil spilled, 2) dose of oil, 3) physiography of the area of the spill, 4) weather conditions at the time of the spill, 5) biota of the area, 6) season of the spill, 7) previous exposure of the area to oil, 8) exposure to other pollutants, and 9) treatment of the spill. Several of these factors are touched upon below.

Natural Physical Processes Affecting Oil in the Water Column

Once oil is spilled, it is dissipated by evaporation, dissolution, and mixing or dilution in the water column. The natural processes are speeded by wind action and by waves and currents that increase spreading and vertical mixing. Various fractions respond differently to these processes, and the weathered residue behaves differently than the material originally spilled. A contaminated bay may be flushed by freshets, tidal action, or longshore currents. Some oil sinks directly to the bottom, especially in fresh water, where some oil fractions have densities approaching that of fresh water, and in water with high sediment loads. Certain fractions may undergo autoxidation.

Conover (1971) reported that sedimentation of fecal-bound oil that had been ingested by zooplankton may have accounted for up to 20% of the spilled oil entering the water column at Chedabucto Bay, Nova Scotia. Oil can also be removed from the water column by absorption within organisms and accumulation within the food chain. Suspended sediments carried by runoff from a major flood entered the Santa Barbara Channel area immediately before and after the well blowout (Kolpack, 1971). Kolpack noted that adsorption of oil on the flocculated suspended particles followed by decomposition was a major factor in carrying much of the oil to the sea floor. Kinney et al. (1970) reported, however, that in Cook Inlet, Alaska, glacial silt from the inlet had no apparent effect on the emulsion properties or the sinking of the type of crude oil found in that area.

Forrester (1971) noted the extensive distribution of oil particles stirred into the water by wave action after a bunker C oil spill in Chedabucto Bay. Oil particles were found to a depth of 80 m inside the bay and to depths of 45 m at a distance of 65 km outside the bay. Near-surface distribution of particles extended 250 km southwest along Nova Scotia in a band extending up to 25 km offshore. Berridge, Thew, and Loriston-Clark (1969) indicated that the stabilization of emulsions like those observed at Chedabucto Bay and elsewhere was caused by complex chemical components in the nonvolatile residues and not by bacterial activity, marine organisms, or suspended solid matter.

Environmental Differences

The fate and effects of oil spilled in the marine environment are difficult to generalize because several types of environments may be involved. Some extreme comparisons are tropics versus arctic, open ocean versus estuaries, and the differences between the intertidal and subtidal zones.

Within these environments are several diverse physical conditions such as temperature, salinity, oxygen, and nutrient concentrations, as well as biological differences such as species composition, diversity and density, and community metabolic rate. The prediction or assessment of pollution effects on the basis of observations extrapolated from one environment to another is seldom supported by adequate data. Unfortunately, however, few data on pollution effects exist for most areas and species, which has led to the use of information from areas that may be dissimilar in critical respects.

There are arguments as to which environment is the most stable and capable of withstanding attacks by additional pollution stresses. Copeland (1970), discussing the response of ecological systems to stress, suggested the principle that ". . .those systems already subjected to energy-requiring stresses are more likely to resist the changes than those (such as tropical systems) adapted to relatively constant environments." He concluded that estuarine ecosystems composed of organisms capable of wide adaptations and generalizations, such as north temperate systems, would be relatively unaffected by the same magnitude of disturbance that would drastically alter

a tropical system. Odum (1970) noted, however, that many estuarine species are living near the limit of their tolerance range and that any alteration in the environment, such as additional stresses caused by low levels of pollution, could exclude these animals permanently from the estuary.

All healthy balanced ecosystems are generally functioning at or near some critical tolerance limit. In an ecosystem with a variable environment, such as a north temperate estuary, responses to additional stress might not always be the same. For example, even though factors surrounding an oil pollution incident might be outwardly similar in most respects to another spill in a comparable area, the biological impacts may differ. The ability of the local community to absorb the additional stress will be influenced by the coincidence of seasonal variability of natural stresses, the differences in vulnerability of stages in an organism's life cycle, and many other dynamic features of the ecosystem.

Biological Differences

The effects of oil pollution on many different organisms in various habitats may vary from no effect to responses of avoidance and decreased activity, to nonadaptive responses of panic and physiological stress. What kills one species may have little or no effect on another. Affected organisms vary from single cells, to sedentary clams, to highly mobile predators, each of which has different behavioral and physiological interactions with the environment.

Just as different species are affected differently, so may individuals within a species be affected differently. In particular, different life stages such as eggs, hatched larvae, and newly molted individuals may have different sensitivity to the same level of pollution. Mironov (1968), for example, reported that prelarval stages of barnacle, *Balanus* sp., were 100 times more sensitive to oil pollution than the adult form. This contrasts with the relative lack of sensitivity to crude oil by pink salmon eggs and sac fry, which were 10 times more tolerant than older fry (Stanley D. Rice and Adam Moles, Auke Bay Fisheries Laboratory, National Marine Fisheries Service (NMFS), NOAA, Auke Bay, AK 99821, pers. commun.).

Renzoni (1973) conducted a series of experiments on the toxicity of several crude oils and petroleum products to the sperm, eggs, and larvae of the oysters *Crassostrea angulata* and *C. gigas* and the mussel *Mytilus galloprovincialis*. He found a relatively high degree of tolerance by eggs and larvae but reported that the fertilizing capacity of sperm was markedly affected by similar exposures.

Biodegradation

Quantitative data describing the biodegradation of various components of crude oil, especially in arctic and subarctic areas, are limited.

ZoBell (1973a) briefly reviewed the current understanding of microbial degradation of oil, including interactions, limiting factors, problems, and perspectives. Ahearn (1973) stated that research on microbial utilization of hydrocarbons for treatment of oily pollutants in the environment, though more intensive in recent times, is still in an early stage of development. It is known that microorganisms can degrade much of a crude oil, particularly the less toxic paraffinic compounds. No single species can degrade all the compounds, but many different species together can metabolize a large number of the compounds, if not all. The rate of microbial degradation, which is principally aerobic, decreases with a decrease in temperature. Large quantities of oxygen are needed. It has been estimated, for instance, that complete oxidation of 1 gallon of crude oil would require all of the dissolved oxygen in 320,000 gallons of water. This comparison may be unrealistic because most oil is at the surface of water in contact with air and only the outer surfaces of oil can be attacked at any one time. It is reasonable to assume, however, that an oxygen-deficient environment may well occur under some oil slicks and in oil-contaminated sediments.

Glaeser and Vance (1971) studied the behavior of Prudhoe Bay crude oil in controlled spills in the Chukchi Sea but were not able to isolate any microorganisms which could degrade hydrocarbons at the ambient temperatures of the Arctic, although some emulsification of the crude oil was observed. However, ZoBell and Agosti (1972) collected oil-oxidizing bacteria near natural oil seeps from the Alaska North Slope and observed oxidation rates of mineral oil at –1°C and above. They noted that the solid surfaces of the ice crystals appeared to facilitate bacterial growth, because the rate at –1°C was substantial and near the 4°C rate.

The apparent contradiction between the studies is probably best explained by ZoBell's (1973b) continued observations with North Slope bacteria. He

found that the nine different crude oils were not degraded as rapidly as purified mineral oil. Glaeser and Vance's studies were with microorganisms from the surface water of the Chukchi where small numbers of bacteria may have been present. Furthermore, the observations of Straughan (1971), who noted the apparent lack of biological damage by the Santa Barbara blowout, may apply here. She discussed the possibility that the fauna had an unusually high tolerance for oil, probably because of adaptation from chronic low-level oil exposures from local natural seepages. The observations of ZoBell and Agosti (1972) on the oxidation rates of oil at −1°C may be an example of similar adaptive response by the North Slope bacteria collected near natural seeps. These oxidation rates and other adaptive responses might not occur from organisms that have not been preacclimated to chronic low-level exposures of oil and may explain why Glaeser and Vance obtained reports of negligible oxidation rates at 0°C from microorganisms from surface water of the Chukchi Sea. Robertson et al. (1973) estimated hydrocarbon-oxidizing bacteria populations were in the order of 1/ml in Cook Inlet and Port Valdez, but less in the Arctic Ocean. Numbers decreased with salinity in Cook Inlet and with depth in Port Valdez.

ZoBell (1963) reported that oil is readily adsorbed by clay and silt and suggests that although adsorption of oil by solids renders the oil more susceptible to autobial and microbial oxidation, almost no bacterial decomposition occurs after burial in the bottom sediments, probably because the environment is anaerobic. Blumer and Sass (1972) found that some paraffinic hydrocarbons remained in bottom sediments 2 yr after the West Falmouth oil spill and aromatic hydrocarbons were prominent, which suggests that these more toxic compounds are utilized by bacteria to a minimum degree.

Oil in Sediments

The effect of oil in sediments is poorly understood, although several authors have quantitated oil concentrations and noted its persistence. Scarratt and Zitko (1972) observed little diminution of bunker C oil concentration from soft sediments 26 mo after the wreck of the tanker *Arrow*. The oil reached maximum concentrations in coarse sediments 1 yr after the spill, but the concentrations reduced thereafter. Chemical degradation can occur but is normally restricted to the surface layer of the bottom penetrated by ultraviolet light. Blumer and Sass (1972) noted that "The preservation of hydrocarbons in marine sediments for geologically long time spans is one of the accepted key facts in current thought on petroleum formation." However, in spite of the stability of hydrocarbons in marine sediments, there are characteristic differences between the hydrocarbons in polluted and unpolluted areas. Tissier and Oudin (1973) found that hydrocarbons in polluted sediments differed from those of unpolluted sediments by having lower percentages of heavy components, by not having an odd carbon dominance in the n-alkanes, and by having polycyclic aromatic hydrocarbons with alkyl chains.

Oil residues were observed on sandy beaches by ZoBell (1963) and in marshes and in sediments of the deepest area (15.3 m) near the West Falmouth spill by Blumer, Sass, Souza, Sanders, Grassle, and Hampson (1970).[4] About 2 wk after fuel oil was spilled at Resolute Bay, Northwest Territory, in August 1970, casual sampling revealed that oil penetrated into beach material to a depth of about 3 inches (7.6 cm) (Barber, 1971). Oil may be buried and stay intact for a considerable time, even at the higher temperature of the California coast (ZoBell, 1963). During laboratory experiments, Johnston (1970) determined oil decay rates in sand columns contaminated with various concentrations of oil. Ten percent of the oil was oxidized over a period of several months; the remaining 90% decayed much slower.

The West Falmouth spill provided a unique opportunity for a study of the immediate and long-term effects of an oil spill on an area where the previously existing environmental base was well known (Blumer, Sanders, Grassle, and Hampson, 1971). One effect of the oil was to reduce the cohesion of bottom sediments of tidal marshes and the estuary by killing the benthic plants and animals (Blumer, Sass, Souza, Sanders, Grassle, and Hampson, 1970, see footnote 4). The resulting erosion spread hydrocarbons to new areas, where the process was repeated. Because of the stability and persistence of the hydrocarbons in marine bottom sediments, Blumer, Souza, and Sass (1970) noted that hydrocarbons may be returned to the biosphere by organisms living and feeding in the sediments. This redistribution of hydrocarbons can be

[4]Blumer, M., J. Sass, G. Souza, H. Sanders, F. Grassle, and G. Hampson. 1970. The West Falmouth oil spill. Unpubl. manuscr. Woods Hole Oceanogr. Inst., Ref. No. 70-44, 32 p.

the source of a chronic pollution problem near that spill.

It is quite possible that normal functions of sediments will be disrupted when contaminated by oil. Changes in the sediments that are subtle and difficult to detect, such as decreased nutrient recycling and community metabolism, could result in the loss of significant contributions to the productivity and stability of an area. Although oil in sediments has been monitored and measured after several spills, other aspects of the oil–sediment relation have yet to be studied.

BIOLOGICAL EFFECTS OF OIL POLLUTION

Blumer (1970, see footnote 3) summarizes the potential damage to organisms from pollution by crude oil and oil fractions as follows:

1. Direct kill of organisms through coating and asphyxiation.
2. Direct kill through contact poisoning of organisms.
3. Direct kill through exposure to the water-soluble toxic components of oil at some distance in space and time from the accident.
4. Destruction of the generally more sensitive juvenile forms of organisms.
5. Destruction of the food sources of higher species.
6. Incorporation of sublethal amounts of oil and oil products into organisms (resulting in reduced resistance to infection and other stresses—the principal cause of death in birds surviving immediate exposure to oil).
7. Incorporation of carcinogenic and potentially mutagenic chemicals into marine organisms.
8. Low-level effects that may interrupt any of numerous events (such as prey location, predator avoidance, mate location or other sexual stimuli, and homing behavior) necessary for the propagation of marine species and for the survival of those species higher in the marine food web.

Some of the potential effects described by Blumer may be obvious, such as the direct deaths from acute exposures. Less obvious indirect deaths may occur from effects at either the individual or population level. Individual organisms subjected to sublethal exposures may undergo an "ecological death" if they are less capable of adjusting to and responding to natural changes (stresses) in their physical and biological environments. For example, postmolt Tanner (snow) crab, *Chionoecetes bairdi,* lost legs during short exposures to crude oil (Karinen and Rice, in press). Even though the crabs lived through the exposure, they probably could not have survived in the natural environment because some of them lost as many as seven legs, including both chelae. Moreover, crabs or other adversely but sublethally affected organisms would be more likely to be eliminated by natural selection.

Effects from chronic exposure may be adverse to a population over a period of time if exposed but normal-appearing adults have their ability to reproduce seriously impaired. This loss may be due to physiological changes such as reduced fecundity and delayed ovary development or to impaired behavioral mechanisms which could prevent mate location and identification or homing and timing of spawning. Although the effects at this level might not result in death of the adult, they could induce a trend of decreasing numbers that might eventually eliminate the population or race.

Hydrocarbons in the Marine Food Web

Blumer (1967, 1969) and Blumer, Guillard, and Chase (1971) studied the fate of organic compounds in the marine food web. They found that certain hydrocarbons, even highly unsaturated ones, are stable once they are incorporated into a particular marine organism and that they may pass through many members of the marine food web without alteration and may actually be concentrated in tissue. Most hydrocarbons are lipid soluble and thus may accumulate in food webs to the point where toxic levels are reached. This pathway is illustrated by the well-documented chlorinated hydrocarbon group of pesticides.

The entrance of oil-derived hydrocarbons into marine food webs has been observed several times at several trophic levels. Conover (1971) reported that 10% of the bunker C oil in the water column after the Chedabucto Bay spill was combined with zooplankton and that their feces contained up to 7% oil. Mironov (1968) also noted the ability of some zooplankters to accumulate hydrocarbons. The incorporation of hydrocarbons into the food web at these primary levels assures exposure at all higher trophic levels.

Blumer, Souza, and Sass (1970) and Ehrhardt (1972) reported pollution-derived hydrocarbons in shellfish. Uptake and retention of labeled hydrocarbons of several classes by a marine mussel,

Mytilus edulis, was noted by Lee, Sauerheber, and Benson (1972). Smith (1968) reported the presence of oil and benzene-ring compounds in the feces of limpets browsing on an oily deposit, and in top shells, *Monodonta*, and limpets, *Patella*, living on oiled rocks. He reported that analysis of the gut indicated "the proportion of oil in material ingested by these animals was estimated as about 20-30 percent in *Patella* and 5-50 percent in *Monodonta*."

Organisms at the highest trophic levels may be affected directly by the oil itself or indirectly by hydrocarbons that have reached them through the food web. Horn, Teal, and Backus (1970) found large amounts of tar in the stomachs of three saury, *Scomberesox saurus*, from a sample of ten in the Mediterranean Sea near Gibraltar. Although saury are generally considered to be carnivorous, the occurrence of tar and also of "vegetable debris" in one of the stomachs examined by Horn et al. (1970) suggests that the species is not a very discriminate feeder. Although all ingested oil was obviously not incorporated into the tissues (some oil was found in feces), such feeding behavior does describe a pathway for hydrocarbons to be directly taken up into the tissues of the organism. Thus, oil ingested, absorbed, and even adsorbed may enter the food chain when contaminated organisms are eaten.

Carcinogenicity

Some doubt may remain as to the direct carcinogenicity to man of crude oil and crude oil residues in marine organisms (Blumer, 1969), but evidence pointing toward this is accumulating (Blumer, 1970, see footnote 3; 1972). A literature search and evaluation conducted for the U.S. Coast Guard by Battelle Memorial Institute (1967) noted that shellfish, although alive, may have been unfit for consumption because of the carcinogenic hydrocarbon 3, 4-benzpyrene in their bodies. Oysters that were heavily polluted and contaminated with ship fuel oil were reported to contain 3,4-benzpyrene. The Battelle review also reported that barnacles attached to creosoted poles contained the same carcinogenic hydrocarbon (3,4-benzpyrene). Sarcomas were elicited when extracts from the barnacles were injected into mice. The endemic occurrence of papillary tumors around the rectal opening of soft-shell clam, *Mya arenaria*, was reported, but the author (Battelle Memorial Institute, 1967) did not feel these were due to oil pollution, even though the clams were taken from waters adjacent to areas highly polluted by ship fuel oil. Hyperplasia in reproductive cells of a bryozoan in response to coal tar derivatives was observed by Powell, Sayce, and Tufts (1970). They noted that similar abnormalities may also have occurred in coastal faunas exposed to spills such as the *Torrey Canyon* and the Santa Barbara blowout. However, most observations on these spills were concerned with gross mortality and may not have detected the sublethal effects.

ZoBell (1971) reported the natural synthesis and metabolism of carcinogenic hydrocarbons by several marine organisms. Thus, oil pollution is certainly not the only source for carcinogenic hydrocarbon introduction into marine food webs. Suess (1972) recognized that carcinogens were in seafoods but concluded that they would probably not be dangerous unless the foods contained an excess amount of polynuclear aromatic hydrocarbon carcinogens. Carcinogenesis from oil-contaminated marine organisms has not been proved, but Ehrhardt (1972) expressed a need for carcinogenic testing of hydrocarbon fractions extracted from marine organisms contaminated by exposure to oil.

Observed Toxic Effects

A study of the available information on potential toxic effects of oil pollution reveals more unknowns than proven conclusions. Only a decade ago, ZoBell (1963) reviewed the literature on the effects of oil on bacteria and higher organisms and concluded that oil pollution had no great adverse impact on fishery resources in general. He did point out, however, a few reports of toxic effects, tainting of flesh, and damage to vessels and fishing gear.

The quantity of literature on effects of oil spills has increased since the *Torrey Canyon* incident of 1967. Most of the recent work has depended on onsite visual surveys after occurrence of an oil spill rather than on experiments and detailed study. The surveys have been limited mostly to the effects of oil and of cleaning or dispersing agents on primarily adult intertidal organisms and populations. These observations on a restricted segment of the affected ecosystem include only a few of the factors that influence the total impact of oil. Wilson, Cowell, and Beynon (1973) noted that the absence of results from studies at the commu-

nity level make the interpretation, extrapolation, and use of many observations very difficult. Further, the differences between various crude oils and between the hundreds of petroleum products in their physical and biological effects must always be kept in mind. Comparative data generally are far too few to permit attaching any relative significance to production area or product formulation in this review.

Field Investigations

The utility of many "after-the-fact" studies is limited because of the lack of knowledge of prespill conditions. Data are often collected without proper controls for comparison, and knowledge of natural local fluctuations and species composition of animal populations is usually quite limited. For these reasons conclusions about the impact of a particular spill may vary.

Ehrsam (1972) reported substantial immediate kills of marine life from a fuel oil spill at Anacortes, Wash., and concluded that if larval and juvenile forms of certain organisms were killed, the full impact of the spill may not be known for some time. Katz (1972) observed intertidal transects of the same affected area and concluded that the effects were minor and long-term effects would be unlikely. Webber (1972) pointed out, however, that these after-the-fact studies observed only a small wedge of the total biota. Knowledge of subtidal and benthic organisms as well as larvae and juveniles was lacking.

Other large spills have been studied in greater detail and have contributed significantly to our understanding of the gross effects of oil. Yet, they have been unable to answer many important questions on the effect of pollutant hydrocarbons in the marine environment, and generalizations learned from one spill may not apply to another because each is different.

Field observations of behavior and effects of oil in Arctic ice environments are few. The U.S. Coast Guard investigations in the Arctic have primarily been directed toward gaining knowledge to improve cleanup methods (Glaeser and Vance, 1971; McMinn and Golden, 1973). Campbell and Martin (1973) discussed possible large-scale movements and persistence of oil spilled in the Beaufort Sea. They suggested that the surface waters of the Arctic Ocean and the winter waters of Chedabucto Bay, Nova Scotia, might be comparable, particularly with regard to the physical behavior of oil. Chedabucto Bay is the site of the grounding of the tanker *Arrow* in February 1970 with 2.8 million gallons of bunker C oil aboard. Campbell and Martin (1973) found that highly stable oil-water emulsions formed to a depth of 50 m throughout Chedabucto Bay. They described conditions by which oil reaching the edge of the pack ice could be distributed under the ice.

Thomas (1973) also suggested that results of the studies at Chedabucto Bay might in some respects be applicable to spills in the Arctic. He observed remobilization of oil from beneath the weathered surface of deposits during the summers following the *Arrow* spill and the subsequent re-oiling of some intertidal areas, adding a chronic pollution aspect to the spill. Extensive mortalities of soft-shell clams and salt marsh cord grass, *Spartina alterniflora*, resulted where this occurred. In other areas, clams were visibly contaminated with oil and clam fishing was closed, at least through the summer of 1972 (Thomas, 1973).

When the *Torrey Canyon* broke up near the southwest coast of England in 1967, 15 million gallons of Kuwait crude oil with a high aromatic content were released. Efforts to cope with this first super disaster depended principally upon 2 million gallons of toxic dispersant, which probably caused more damage than the oil, most of which had weathered at sea for a week or more before reaching the shores. Many techniques for oil containment and control on the seas were attempted during the time oil leaked from the tanker; the fact that they all failed reveals the inadequacies of our technology and preparedness for such emergencies.

Extensive investigations of the West Falmouth spill by Blumer and his associates at Woods Hole provide one of the best documentaries of an oil spill. A total of 185,000 gallons of no. 2 fuel oil (41% aromatic content) were spilled in 1969 from a ruptured barge. Intertidal and subtidal benthic organisms of all phyla were killed during the first few days (Blumer and Sass, 1972). Blumer, Souza, and Sass (1970) showed that the uptake of fuel oil hydrocarbons by shellfish left them unfit for human consumption. Later, Blumer and Sass (1972) reported the continued persistence of fuel oil hydrocarbons in the sediments after 2 yr. Although there had been some degradation, the boiling range and composition of the hydrocarbon mixture was basically unchanged.

The 1969 Santa Barbara blowout released an estimated 5,000 barrels of crude oil per day ini-

tially (Foster, Charters, and Neushul, 1971), yet biological damage was not reported widespread and the area has started to recover. Foster, Neushul, and Zingmark (1971) observed that much of the damage to intertidal areas corresponded to sand movement, probably from storm damage. Cimberg, Mann, and Straughan (1973) concluded that the blowout had less effect on intertidal marine organisms than did sand movement and substrate stability. Straughan (1971), reporting on investigations at Santa Barbara, noted factors unique to that accident: 1) the long history of natural oil seepage in the Santa Barbara Channel and 2) the unusually heavy winter runoff at the time of the spill, which reduced salinities, increased sedimentation, and possibly increased pesticides in the channel. R. L. Kolpack (pers. commun. cited by Kanter, Straughan, and Jessee (1971)) noted that Santa Barbara crude oil is relatively insoluble in seawater and contains a very low percentage of the toxic aromatic compounds. Thus, information gathered on the effect of the Santa Barbara spill or any other is of limited utility in predicting the ecological effects of crude oil spills or of other oils in other areas.

Several studies have provided encouraging reports of varying degrees of recovery after some of the recent larger spills. Investigations about 1½ yr after the *Torrey Canyon* spill revealed that at least the affected shoreline areas were recolonizing and recovering, although recovery was not yet complete at that time (Spooner, 1969). The areas affected by the 1969 Santa Barbara blowout were recently reported to be recovering (Cimberg et al., 1973), as was a reef affected by bunker C oil spilled from a tanker collision in San Francisco Bay in January 1971 (Chan, 1973).

Too few of the controlled field investigations have been designed to bridge the gap between field surveys after spills and simulative laboratory experiments. Perkins (1970) exposed periwinkles and other intertidal organisms to the oil dispersant BP1002 in the laboratory and then released marked individuals in the natural environment. After recapture of the individuals exposed, he found that survival from doses as low as one three-thousandth of the 24 h LC_{50}[5] was lower than among the recaptured controls. Crapp (1971a) conducted field experiments by applying crude oil and oil emulsifiers to the intertidal zone. Physical damage by the oil was observed, but toxicity damage was not great because the oil had previously been exposed to air; in contrast, the oil-emulsifier mixtures were toxic. Baker (1970) applied a crude oil to salt–marsh plots at different times of the year and monitored the effects on plants. Summer applications of oil severely affected annuals but not perennials.

[5]24 h LC_{50} equals that dose of toxicant that resulted in 50% survival after 24-h exposure.

Laboratory Studies

Experiments in the laboratory also do not provide all the answers about how an oil spill will affect a marine organism or its environment. Laboratory research has demonstrated the toxicity of various crude oils and petroleum products on several forms of marine life. Much of this research has focused on the planktonic life history stages of pelagic and benthic animals. Many of these planktonic larvae are phototactic at their earliest stages and concentrate in the surface layer of the sea. This community of the surface 5 cm, the neuston, is the first affected by most oil entering the water. Thus, many organisms are most sensitive to oil pollution at the time of their greatest likelihood of exposure.

Studies by Mironov (1968) on the development of fertilized eggs of the plaice, *Rhombus macoticus*, showed extreme sensitivity of the eggs to the influence of the oil products in seawater. He noted that injury to the eggs occurred at concentrations of 10^{-4} to 10^{-5} ml/liter (0.1 to 0.01 ppm). In these concentrations of oil products, 40 to 100% of the hatched prelarvae showed some signs of degeneration during development and perished. Mironov (1969a) also demonstrated that 0.001 ml of crude oil per liter was toxic to the eggs of anchovy, scorpionfish, and sea parrots from the Black Sea.

Newly set spat of *Elinius modestus*, an Australian barnacle introduced to Europe, were tolerant of 100 ppm crude oil but showed reduced cirral activity and retarded shell growth (Corner, Southward, and Southward, 1968). Adults of this species also showed reduced activity at 100 ppm (Corner et al., 1968).

Mironov (1969b) tested crude oil on several copepods and a cladoceran, and found that 0.001 ml/liter accelerated death in all forms and that 0.1 ml/liter caused death in less than 1 day. *Acartia* and *Calanus* died at 0.01 ml/liter oil in seawater in 72 to 96 h (Mironov, 1968). Larvae of crab and shrimp died at 1 ppm (Mironov, 1969c).

Little is known of the mechanisms of various

toxic effects. Damage to cell membranes and the cellular contents of planktonic larvae may occur. Goldacre (1968) demonstrated such cytological damage and death to the freshwater protozoan, *Amoeba proteus*, exposed to crude oil fractions. Brocksen and Bailey (1973) measured increased respiratory response of striped bass and chinook salmon to sublethal concentrations of benzene. The fish recovered to normal activity when they returned to noncontaminated water for several days. Rice and Short were unable to demonstrate changes in the enzyme activity of cholinesterase or Na-K stimulated ATPase in juvenile pink salmon, *Oncorhynchus gorbuscha,* after in vivo and in vitro exposures to Prudhoe Bay crude oil (Stanley D. Rice and Jeffrey Short, Auke Bay Fisheries Laboratory, NMFS, NOAA, Auke Bay, AK 99821, pers. commun.). This is somewhat surprising because various hydrocarbon pesticides have been shown to affect both enzymes.

Cellular membranes of phytoplankton are also damaged by the penetration of hydrocarbon molecules: the cellular contents are extruded, and oil penetrates into the cell. Detergents administered in a concentrated solution also penetrate the plant cells and cause the dissolution of cellular membranes and the extrusion of cellular fluid (Ruivo, 1972). The effects of oils on plant respiration are variable, but an increase of respiration is frequently observed, probably because of an alteration of the mitochondria. This could result in an uncoupling of the oxidative phosphorylation enzymes from the electron transport enyzmes, and the energy release would be lost as heat.

All marine animals ultimately depend on the photosynthetic activity of phytoplankton and algae for the production of biomass. Baker (1971), reviewing the literature, noted that weathered *Torrey Canyon* oil had no apparent effect on the photosynthetic activity of green algae. He did find, however, that green algae treated with fresh crude oil died and that photosynthesis in kelp, *Macrocystis* sp., was reduced when the kelp was exposed to various petroleum products. Kauss et al. (1973) determined the effects of crude oil on several species of freshwater algae in both field and laboratory experiments. In their field studies, response of the algae to a spill varied from suppression of growth to its stimulation. In their laboratory studies, they noted depressed photosynthetic rates in one algal species after it had been exposed to aqueous crude oil and other selected aromatics.

Growth of phytoplankton from axenic cultures and mixed cultures of natural populations was inhibited by water-soluble extracts from no. 2 fuel oil in a laboratory study by Nuzzi (1973). Mironov and Lanskaya (1968) demonstrated that marine phytoplankton vary several orders of magnitude in sensitivity to crude oils and kerosene in oil concentrations ranging from 0.1 to 1,090 ppm. Of the 20 species tested, a diatom, *Ditylum brightwellii*, was the most sensitive. The wide variation in susceptibility may account for the statements in other reviews of low toxicity of crude oils to phytoplankton (Føyn, 1965; Nelson-Smith, 1970) and supports the premise that biological response will differ among species.

Sublethal and Chronic Effects of Oil Pollution

While data are scarce in some of the areas previously discussed, information on the ecological effects of chronic sublethal oil pollution is essentially nonexistent. Observing these effects is difficult because they are not dramatic and may pass unnoticed by the casual observer. A full description would require observations extending over a long period of time.

Lewis (1972), commenting on approaches to the study of chronic pollution, contends "... that without a massive expansion of ecological and reproductive data by simultaneous multidisciplinary studies not only will we be unable to detect the significant long-term changes, but we will even remain unaware of the most suitable or important species and methods to build into a monitoring program."

A few studies concerning sublethal effects on organisms have appeared in the literature. Wells (1972) reported deaths of lobster larvae to exposures of 0.1 ml of Venezuelan crude oil per liter, while larvae exposed to 0.01 ml/liter had poor survival rates and were unable to molt to the fourth stage. Decreased limb (cirral) activity of marine larvae exposed to oil has been reported (Smith, 1968). Kuhnhold (1972), while observing toxic effects of crude oils to eggs of cod and to larvae of cod, plaice, and herring noted that the larvae exposed to oil-contaminated water were unable to avoid well-defined milky clouds of toxic oil dispersions. Blanton and Robinson (1973) observed damage to the gills of specimens of seven species of fish that had apparently been exposed to an oil spill off the Louisiana coast.

Crapp (1971b) observed that fucoid algae replaced barnacle and limpet populations near an outfall where the effluent contained about 20-25 ppm oil from treated ballast water of tankers unloading at Milford Haven. Although the relative oil content was low, the cumulative volume discharged was large (20,000 gallons of oil per year), a situation similar to that which may occur at Port Valdez, Alaska, when the trans-Alaska pipeline is completed.

Blumer (1972) discussed how low-level chronic effects of oil may damage marine organisms because of their dependence on natural organic chemical clues for a variety of functions. Salmon and other fishes utilize organic chemical clues in migrations; predators are attracted to prey by organic compounds at the parts-per-billion level (Whittle and Blumer, 1970); and other organisms may use chemical clues for predator avoidance, selection of habitat, and sex attraction. Blumer (1972) discussed the fears that oil pollution may interfere with these fundamental biological processes by masking or blocking, or by mimicking natural stimuli (resulting in false responses). He cited literature discussing the attraction of lobsters to kerosene and to purified hydrocarbon fractions derived from kerosene and noted that many dead lobsters were washed ashore after the West Falmouth spill. Blumer's fears about interference with chemoreception are further substantiated by the observations of Takahashi and Kittredge (1973) on crab behavior. Crabs, *Pachygrapsus crassipes*, exposed to water-soluble extracts of crude oil failed to exhibit feeding behavior or mating behavior responses when given appropriate chemical stimuli. Inhibition of chemoreception of some motile marine bacteria by a crude oil and several other hydrocarbons has been demonstrated by Walsh and Mitchell (1973).

Rice (1973) performed laboratory tests of avoidance of pink salmon fry to Prudhoe Bay crude oil and observed avoidance of oil at concentrations as low as 1.6 mg/liter. He concluded that salmon fry had the capability of detecting sublethal concentrations of oil and that they might avoid areas contaminated with sublethal levels of oil, which would result in confused and nonadaptive migratory behavior. The effect of chronic low-level pollution in areas such as Port Valdez, the terminus of the trans-Alaska oil pipeline, could be as severe as the total loss of all salmon runs in the local area because of altered behavioral responses to sublethal oil pollution.

CONCLUSIONS

Although crude oil generally should be considered toxic to marine organisms and harmful to their environment, most ecosystems can tolerate some pollution because oil can be dissipated or removed by processes like evaporation, autoxidation, dilution, and biodegradation. However, each organism and environment has a limit to how much oil can be absorbed and metabolized. Catastrophic spills are obviously pollution at a level that ecosystems cannot tolerate without damage. However, if the spills are not continued, the oil will slowly be removed and recovery of the area, at least to some degree, will likely occur. There is some evidence for recovery of some affected individuals.

Assessments of the impact of oil pollution cannot depend solely on evaluation of immediate kills of organisms from acute exposures. Chronic low-level oil pollution can cause subtle changes in organisms and is potentially more dangerous to the ecosystem than dramatic catastrophic spills. For this reason, the effects of chronic pollution warrant intensive study so that they will not be underestimated. The cumulative impact of "ecological death" of individuals which have impaired functions may be quite significant, yet difficult to assess because the death is not tied directly to an acute oil exposure. Equally as dangerous is the potential impact on populations where reproductive processes, adversely affected through physiological or behavioral mechanisms, result in fewer progeny. Chronic pollution may eliminate a species from an area entirely, and once eliminated that species may remain suppressed and may not repopulate the area because of continuing pollution or because its niche has been filled by a more tolerant, possibly less desirable, species.

The adverse effects of oil on animal populations has been of wide concern when stocks of special interest, such as those providing the basis of a sport or commercial fishery, have been involved. It should be remembered that changes in populations of lesser apparent significance will also cause changes in the community because each species population interacts with and is dependent on the rest of the community.

The foregoing review of information does little to simplify or ease the problems of policy makers concerned with marine production and transportation of oil and petroleum products. The weight of

the evidence leaves little doubt that oil poses a serious hazard to living marine resources, that spills and chronic pollution have happened and will continue to occur, and that the interests of the marine environment are best preserved if marine transportation of oil and petroleum products is minimized. The continuing need for new sources and increased amounts of energy, however, limits many of the conservative and prudent alternatives to these hazards. Until research has provided conclusive data, policy makers must continue to rely on these interpretative judgments for much of their guidance in making decisions that can profoundly affect the well being of marine ecosystems.

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ON THE DISPERSAL OF LOBSTER LARVAE INTO THE EAST PACIFIC BARRIER (DECAPODA, PALINURIDEA)

MARTIN W. JOHNSON [1]

ABSTRACT

The seaward drift of phyllosoma larvae of lobsters occurring along the coast and adjacent islands of the eastern tropical Pacific Ocean was studied from plankton collections made jointly by the Scripps Institution of Oceanography, Tuna Oceanography Research Program, and the National Marine Fisheries Service, La Jolla, Calif.

Numerous samples taken with trawl and plankton nets were made across the Equatorial current system in two areas: lat. 15°N-5°S, long. 115°-125°W, and lat. 5°N-15°S, long. 95°-115°W. Many late developmental stages of *Panulirus penicillatus* and *P. gracilis* and a few *Scyllarides astori* were found, all apparently having drifted mainly with the South Equatorial Current over a distance of 1,800 to 2,000 or more nautical miles from their likely origin, the Galapagos Islands or the coast of Central America. A few larvae were found in the North Equatorial Countercurrent. This is at times a possible route for return to the adult habitat, but it is doubtful that any of the larvae that have drifted to the most western survey area will be returned by countercurrents in time for metamorphosis or that they can successfully negotiate the remainder of the expanse of the East Pacific Barrier to reach the mid-Pacific islands.

The present report is essentially a follow-up of a previous survey in which a large plankton collection made by the multiship eastern tropical pacific (EASTROPAC) Project in 1967-68 was used in part to ascertain the systematics and geographic distribution of the pelagic phyllosoma larvae of all of the spiny lobsters (Palinuridae) and slipper lobsters (Scyllaridae) known to inhabit the west coast and offshore islands of Central America, Colombia, and Ecuador (Johnson, 1971). In that survey an extensive area was covered along the coast and seaward both north and south of the Equator to about long. 126°W. It therefore forms the basic groundwork drawn upon in the present report dealing with the phyllosoma larvae taken during a more restricted offshore survey within the same area by the Scripps Tuna Oceanography Research Program (STOR) in cooperation with the National Marine Fisheries Service at La Jolla, Calif., and Honolulu, Hawaii. This offshore "skipjack survey" was designed and initiated in 1970 to study the migrations of young skipjack tuna, *Katsuwonus pelamis*, in the eastern tropical Pacific Ocean (Williams, 1971, 1972). A comprehensive review of the current system and water masses so important to pelagic larvae of the area is given by Wyrtki (1967).

From Point Conception southward to the Gulf of Guayaquil, Ecuador a total of four species of palinurid and two species of scyllarid lobsters occur. In the present survey only the larvae of *Panulirus penicillatus* (Olivier, 1811), *P. gracilis* (Streets, 1871), *P. inflatus* (Bouvier, 1895), and *Scyllarides astori* Holthuis, 1960 were found as expatriate larvae from the coast or coastal islands. *Panulirus interruptus* (Randall, 1840) occurs off the coast of southern and Baja California, too far north for its larvae to be expected to enter into the current system covered here except as rare stragglers in the North Equatorial Current. *Evibacus princeps* Smith, 1869 (the second scyllarid) although common to the eastern tropical Pacific, apparently has a larval period too short to be carried far from the coast (Johnson, 1971). The larvae of *P. gracilis* and *P. inflatus* are difficult to separate specifically if the fourth pereiopods have been lost. However, adults of only *P. gracilis* occur in the southern range including the Galapagos Islands and all but two larvae could be referred to that species. The larvae of *Jasus frontalis* (H. Milne Edwards, 1837) and *Scyllarus delfini* (Bouvier, 1909), the two lobsters found in the Juan Fernandez Islands off Chile, were not found in the equatorial currents or in the Peru Current to lat. 24°S during the EASTROPAC survey and none were taken in the present survey.

The duration of the phyllosoma larval period as derived from studies of different species in

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nature indicate about 8 to 11 mo for palinurids (Johnson, 1960; Lazarus, 1967; Chittleborough and Thomas, 1969). In some scyllarids shorter periods are indicated (Saisho, 1962; Robertson, 1968), but in others, including *Scyllarides astori*, a length comparable to that of palinurids is suggested by the wide dispersal of the larvae.

These long drifting periods provide ample time for far and wide dispersal. Coincident with this, the number of larvae caught in a plankton tow is always small especially for the later stages and this precludes close statistical analysis for short surveys. But the presence of even small numbers of larvae when scattered over a large area or period of time are significant in indicating major outlines of the type of drift and dispersal by currents from adult spawning areas.

PROCEDURE

In view of the scarcity of larvae and the presence of only later developmental stages VI-XI (the final phyllosoma stage) in far offshore waters, the collections most generally useful were those from nets filtering large quantities of water: a 15 × 15 m mid-water trawl with a section of 3-mm bar mesh and towed obliquely in steps from 100 to 0 m or from 30 to 0 m for about 1 h 30 min; and a Blackburn micronekton net 5.8 m long constructed of nylon with mesh apertures of about 5.5 × 2.5 mm, and cod end of no. 56 XXX grit gauze. This net attached to a 5 × 5 foot (1.52 × 1.52 m) frame was towed about 60 min obliquely from 200 to 0 m. Samples were also analyzed from tows taken with a 5-m long "neuston" net constructed of nylon with mesh apertures of about 0.65 mm, and cod end of no. 56 grit gauze. This net was attached to a 1-m ring bent to form a narrow opening and buoyed to tow at the immediate surface for 15 min. For *David Starr Jordan* cruise 65, analyses were also made of all samples taken with a similar net attached to a regular 1-m ring towed obliquely from 200 to 0 m for 20-25 min simultaneously with the neuston net.

RESULTS

David Starr Jordan Cruise 57 and *Townsend Cromwell* Cruise 51 5 Nov.-21 Dec. 1970

In Figure 1 is shown the station pattern

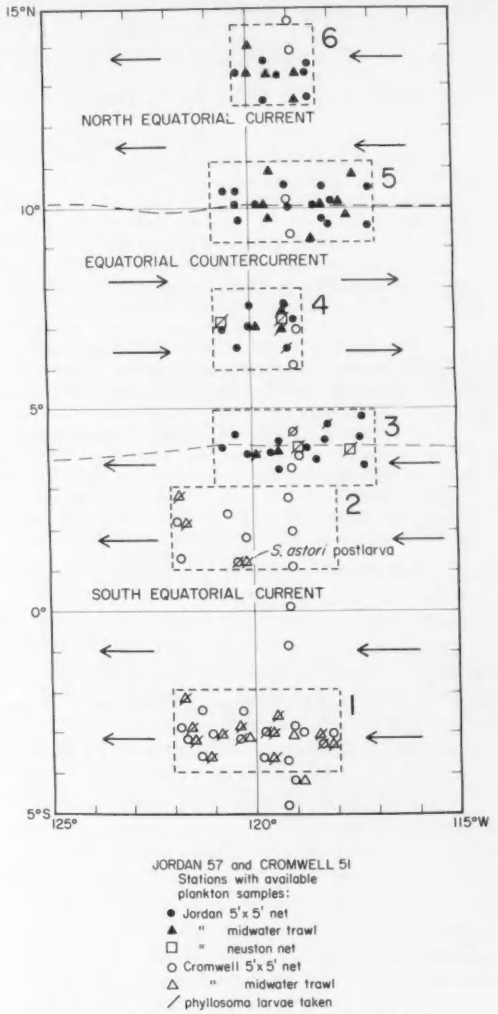

FIGURE 1.—RV *Townsend Cromwell* cruise 51 and RV *David Starr Jordan* cruise 57 station pattern in unit areas 1-6. Neuston net tows are shown only where larvae were taken.

where net tows, positive or negative for phyllosoma larvae, were taken by the trawl or the 5 × 5 foot net. The stations occupied fall into more or less distinct unit areas as designed for the tuna study to correlate with the prevailing major elements of the Equatorial Current System.

The number and stages of larvae caught in the various nets are given in Table 1 for each of

the unit areas. Because of the scarcity of specimens, no attempt is made to give figures based on unit volume of water filtered.

In unit area 1, 52% of 27 tows (other than with the neuston or 1-m net) yielded a total of 87 larvae in this 8° square area in the South Equatorial Current. Nine neuston net tows caught no larvae.

The three stations below 4°S were negative and approach or fall into a large expanse of water that yielded no larvae during the EASTROPAC cruises (Johnson, 1971, Chart 12).

Unit area 2 also in the South Equatorial Current was less well sampled, but 36% of 11 tows with the trawl and 5 × 5 foot net yielded a total of 35 phyllosoma larvae and one scyllarid postlarva (nesto). The five neuston tows were negative.

The large number of larvae caught by the trawl in unit areas 1 and 2 when compared with the more northern unit areas is striking in indicating the tendency of the South Equatorial Current to retain its load of phyllosoma larvae in their long drift from the adult area.

In unit area 3 overlapping into the North Equatorial Countercurrent, which was well developed at the time (Williams, 1971), 20% of 15 tows with the trawl and 5 × 5 foot net were successful but yielded only seven larvae in these nets. However five additional larvae were caught in 2 of 11 neuston tows.

Unit area 4 comprises only a 2° square area within the North Equatorial Countercurrent. Here two of three trawls and one of nine 5 × 5 foot net tows yielded 3 and 1 larvae respectively while the neuston net caught a total of 10 larvae in two of eight tows. The successful neuston tows in this area and in unit area 3 were taken during evening or nighttime tows.

Unit areas 5 and 6 provided no phyllosomas although both areas were comparatively well sampled.

The relatively large number of larvae taken during these two cruises compared with the following cruises reflects more intensive sampling, especially with the trawl, but a seasonality in release of larvae in the adult area may also have contributed.

David Starr Jordan Cruise 60 6 Mar.-11 Apr. 1971

The stations occupied for plankton were more scattered and very few larvae were caught,

TABLE 1.—*David Starr Jordan* cruise 57 and *Townsend Cromwell* cruise 51. Types of gear, total number of tows taken (the successful number of which is shown in parenthesis) and the number of larval species caught with different gear in unit areas 1-6.

Unit areas No. of tows Successful no. in parentheses	Species taken and type of gear	Phyllosoma stages VII	VIII	IX	X	XI	Total larvae in unit area
1	*P. gracilis*, 5′ × 5′		1				
5′ × 5′, 14 (3)	*P. gracilis*, trawl	1	11	18	2		
Trawl, 13 (11)	*P. penicillatus*, trawl			7	16	16	
Neuston, 9 (0)	*S. astori*, trawl	1	1	3	4	6	87
2	*P. gracilis*, 5′ × 5′	1	1				
5′ × 5′, 8 (1)	*P. gracilis*, trawl	2		1	1		
Trawl, 3 (3)	*P. penicillatus*, trawl	1	10	11	6		
Neuston, 5 (0)	*S. astori*, 5′ × 5′		1				
	S. astori, trawl			1			35 + 1 nesto
3	*P. gracilis*, 5′ × 5′	1	2				
5′ × 5′, 13 (2)	*P. gracilis*, trawl	1		1	1		
Trawl, 2 (1)	*P. gracilis*, neuston	1	3	1			
Neuston, 11 (2)	*P. penicillatus*, trawl		1				12
4	*P. gracilis*, 5′ × 5′	1					
5′ × 5′, 9 (1)	*P. gracilis*, trawl			1			
Trawl, 3 (2)	*P. gracilis*, neuston	1	4	5			
Neuston, 8 (2)	*P. penicillatus*, trawl			1	1		14
5							
5′ × 5′, 13 (0)	none						
Trawl, 8 (0)							
Neuston, 11 (0)							0
6							
5′ × 5′, 8 (0)	none						
Trawl, 5 (0)							
Neuston, 8 (0)							0

hence the data on larval distribution, species, and stages taken are entered directly on the chart (Figure 2). The successful tows indicate at least a presence of larvae in all of the major currents traversed. The North Equatorial Current at this time showed a few stage VII *P. penicillatus* with Clipperton Island a likely source of origin.

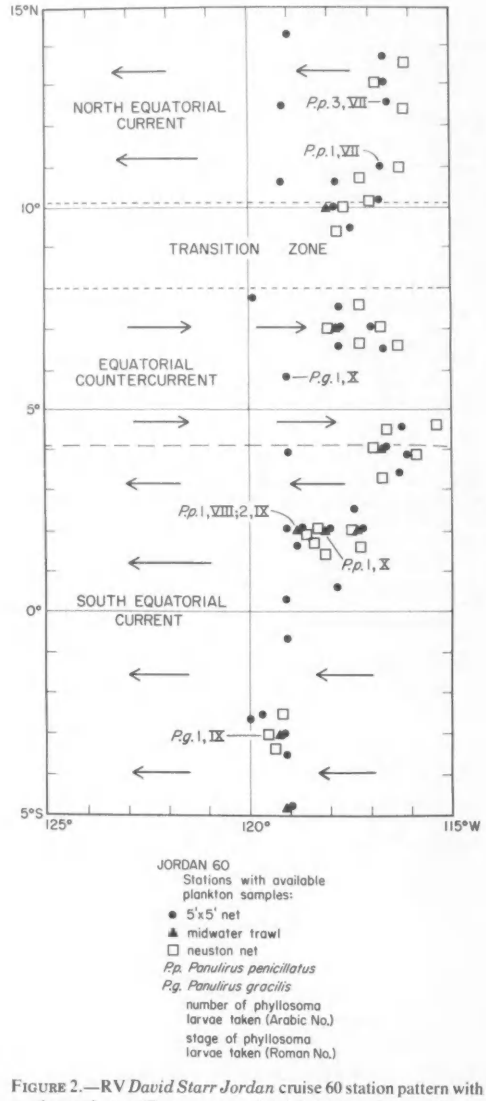

FIGURE 2.—RV *David Starr Jordan* cruise 60 station pattern with number and stage (Roman numeral) of phyllosoma larvae taken at station indicated.

David Starr Jordan Cruise 65 24 Aug.-30 Sept. 1971

As shown in Figure 3, this cruise covered an area much nearer the Galapagos Islands, from which most of the phyllosomas taken probably originated. It also extended less to the north and farther to the south. The data will again be presented here by unit areas (2° squares).

Unit 1 falls below lat. 11°S and yielded no larvae in a total of eight tows (Table 2). It is probable that the area is within the influence of the northern boundary of the western extension of the Peru Current which as already mentioned had few or no phyllosomas during the EASTROPAC cruises.

In unit 2 within the South Equatorial Current, a total of 16 tows with the various nets yielded 19 larvae, mainly by the trawl.

Units 3 and 4 although within the South Equatorial Current had only two and four larvae respectively in a total of 18 mixed tows.

Unit 5 directly west of the Galapagos was the most productive of larvae where five of eight neuston hauls yielded a total of 33 specimens.

Unit 6, still within the South Equatorial Current, was less productive of larvae although three of eight neuston net tows took five larvae.

A total of 35 tows taken with the 1-m net simultaneously with the neuston net during the cruise yielded no larvae whatever (see Discussion).

David Starr Jordan Cruise 77 8 Jan.-17 Feb. 1973

Figure 4 depicts the station pattern across the current system. As in cruise 60 there were so few phyllosoma larvae that it will suffice to record the data relative to these directly on the chart. There were a few scattered palinurid larvae in the North Equatorial Current. The nearest likely source of these being Clipperton Island. A few also occurred in the northern part of the South Equatorial Current. That these probably came from the Galapagos Islands is indicated by the accompanying larvae of *Scyllarides astori*, the adult of which is relatively rare except in that area.

Of special interest however is the occurrence of a single, late stage *Parribacus* sp. phyllosoma in this group of stations. No adult species of this genus has been reported from the west

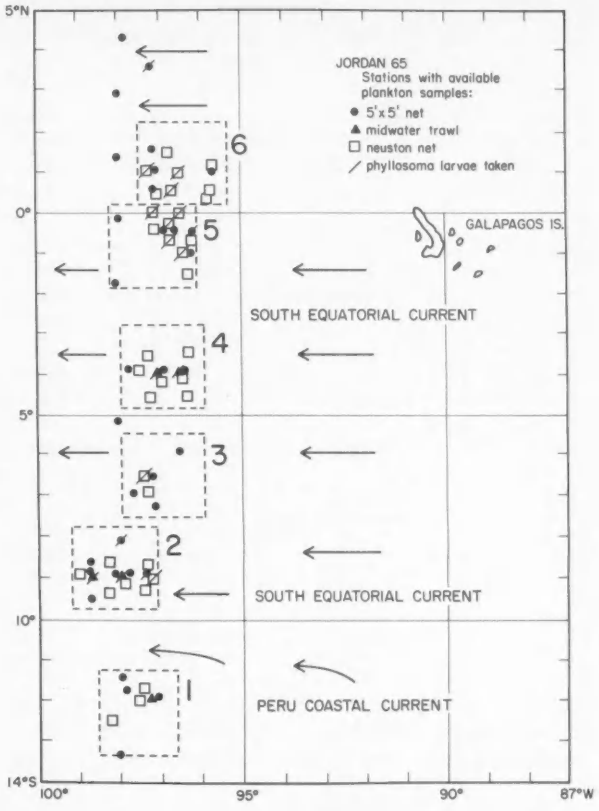

FIGURE 3.—RV *David Starr Jordan* cruise 65 station pattern in unit areas 1-6; 1-m net tow also made at neuston stations.

coast of the Americas. Hence one is forced to conclude that it most likely had drifted from islands to the southwest where the genus is known to occur. It should be mentioned here also that a late larva of this genus was taken at lat. 14°13.6′S, long. 126°00′W near the southern limit of the most distant offshore stations of EASTROPAC. Nothing is known regarding the duration of the entire floating period of this genus.

Saisho (1962) included *Parribacus antarcticus* in his generalization stating that the free-swimming life of scyllarids is shorter than for palinurids. This was based on laboratory studies of only the first three larval stages. However, if the present observations of the two late, but not yet the last, stage is characteristic of the genus they suggest that, like *Scyllarides astori*, the free-swimming life is not abbreviated.

DISCUSSION

This survey is of special interest in substantiating the earlier findings of the EASTROPAC survey relative to the far offshore drift of planktonic stages of lobster larvae in the Equatorial Current System. As in the earlier survey, only species known to occur in the east tropical area were found with one exception (*Parribacus* sp.) referred to above.

Assuming that the Galapagos Islands are the main source of the larvae encountered, it is evident that the westward transport with the South Equatorial Current involves at least a distance of about 1,800 nautical miles. In *Townsend Cromwell* cruise 51 larvae of each of the prevailing species *Panulirus penicillatus*, *P. gracilis*, and *S. astori* were netted in trawl tows at the western-most stations at long. 121°32′-121°54′W between lat. 02°45′N and

TABLE 2.—*David Starr Jordan* cruise 65. Types of gear, total number of tows taken (the successful number of which is shown in parenthesis) and the number of larval species caught with different gear in unit areas 1-6.

Unit areas No. of tows Successful no. in parentheses	Species taken and type of gear	Phyllosoma stages VI	VII	VIII	IX	X	Total larvae in unit area
1							
5′ × 5′, 4 (0)	none						
Trawl, 1 (0)							
Neuston, 3 (0)							0
2	*P. gracilis*, neuston		1	1			
5′ × 5′, 7 (1)	*P. penicillatus*, 5′ × 5′			1	1		
Trawl, 2 (2)	*P. penicillatus*, trawl		5	5	3		
Neuston, 7 (1)	*S. astori*, trawl		1	1			19
3	*P. gracilis*, neuston		2				
5′ × 5′, 4 (0)							
Neuston, 2 (1)							2
4	*P. gracilis*, trawl			4			
5′ × 5′, 3 (0)							
Trawl, 2 (2)							
Neuston, 7 (0)							4
5	*P. gracilis*, neuston	6	14	10	2	1	
5′ × 5′, 6 (1)	*P. penicillatus*, 5′ × 5′		1				
Neuston, 8 (5)							34
6	*P. gracilis*, neuston	2		2	1		
5′ × 5′, 4 (0)							
Neuston, 8 (3)							5
North of unit 6							
Isolated Stn. 229	*P. gracilis*, 5′ × 5′			1			1

02°57′S. During the EASTROPAC survey only *P. penicillatus* was found at the western-most stations at about long. 126°W near the equator, a distance of about 2,000 nautical miles. These *P. penicillatus* larvae might conceivably have drifted eastward from the oceanic islands of the south Pacific where the adult is known to occur. But no other species common to the mid–Pacific islands has ever been found in any part of the eastern tropical Pacific survey areas except for the two specimens of *Parribacus* sp. mentioned previously. Obviously one sees here the working of the East Pacific Barrier towards maintaining a specific separation of west American and Indo–Pacific lobster faunas. *Panulirus penicillatus*, which occurs all the way through the Pacific and Indian Oceans to the Red Sea, is unique among lobsters in having successfully overcome this barrier to become established on offshore islands, but appears to have found additional barriers that prevent establishment on the coast of the mainland. George (1969) interprets this as a failure to compete successfully with the east Pacific mainland species that have evolved there by natural selection. The absence of *P. penicillatus* in the coastal environment may result largely from elimination of the larvae by an admixture of inimical coastal water as they approach the coast. This supposition is suggested by the fact that no larvae of this species have thus far been found at stations near the coast despite their capability of wide dispersal offshore.

Other crustacea with relatively shorter planktonic lives appear also to have migrated eastward across the East Pacific Barrier (Chace, 1962; Garth, 1966).

The countercurrents within the Equatorial Current System provide possible routes for return of east Pacific species that have either fortuitously or through instinctive behavior shifted into countercurrents, possibly through habits of diurnal migrations, and that have not drifted westward to a point of no return determined by requirements inherent in their life cycle.

To evaluate how effective these return routes may be needs further study based on plankton collections designed to elucidate the vertical distribution of the larvae and the diurnal migrations that they undergo in relation to light, etc., and to the depths of prevailing countercurrents in relation to adjacent currents. In this connection it is

useful to examine the results of certain neuston and 1-m net tows, especially those taken during *David Starr Jordan* cruise 65 where 28.5% of 35 neuston tows yielded one or more larvae, and two tows contained eight and nine larvae respectively. All but two of the neuston tows that were positive for larvae were taken during dusk or darkness. The 1-m net tows taken simultaneously from 200 to 0 m yielded no larvae in either the nighttime or daytime tows. This discrepancy is rather surprising and the cause is not clear. But it may indicate that larvae are so scarce and widely dispersed vertically at depth that the 1-m net does not filter enough water to be effective at depth and its passage through the immediate surface layer is very brief, whereas the neuston net, although filtering less water, caught larvae because of their active concentration in a very narrow horizon at the very surface during conditions of reduced light. Other observations in the field (Chittleborough and Thomas, 1969) and in laboratory experiments (Ritz, 1972) demonstrate this behavioral response of phyllosoma leading to a migration into surface layers at night.

In *David Starr Jordan* cruises 57 and 60 the trawl and neuston tows show that larvae do get into the North Equatorial Countercurrent (Figures 1 and 2). This is an expected correlation with the physical studies of the countercurrent which indicate that some variable transverse circulation does occur across the current such that water is drawn in at the surface along the southern boundary and a loss occurs across the northern boundary (Wyrtki, 1967). The Equatorial Undercurrent at the Equator is another possible route for return to the Galapagos and surrounding area.

Williams (1972), in presenting a hypothetical model of an eastward passive migration of skipjack tuna from the central Pacific spawning area in recruitment of the fisheries in the eastern Pacific, has reviewed hydrographic details relative especially to the position, speed, and seasonal interruptions of the North Equatorial Countercurrent. The seasonal fluctuations of this current could aid or retard the passive migration of tuna larvae and juveniles from the spawning grounds depending upon the degree of coordination with the season of spawning. Much of this transport mechanism might apply also to the return of the long-lived lobster larvae. But it is not known if there is a significant seasonality in the release of the larvae in the adult habitat that might fortuitously correlate with the North Equatorial Countercurrent and thus enhance the likelihood of return of larvae that have drifted to the west. Data from EASTROPAC suggest a very long breeding season for the tropical species as judged by the persistent occurrence of early larval stages (III-IV) in

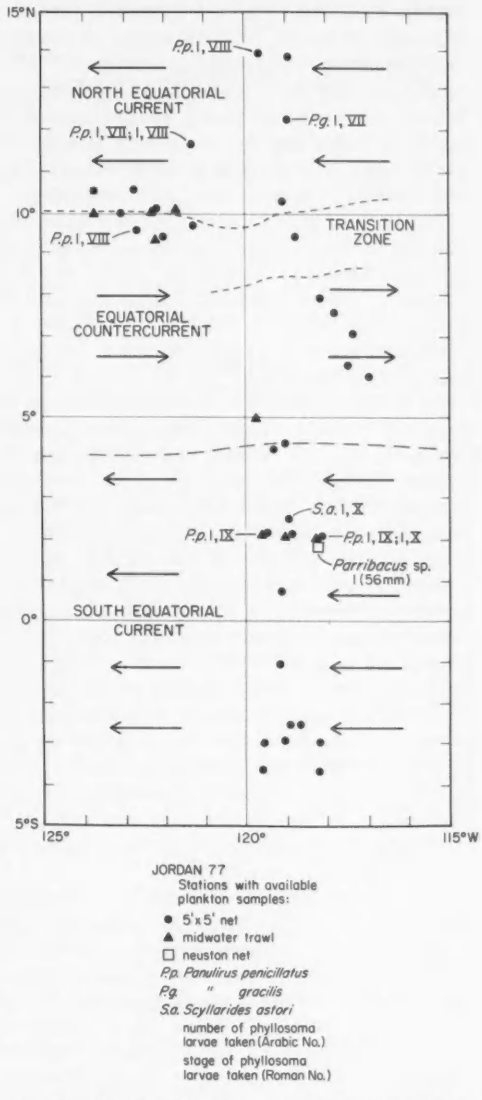

FIGURE 4.—RV *David Starr Jordan* cruise 77 station pattern with number and stage (Roman numeral) of phyllosoma larvae taken at station indicated. Neuston net tow is shown where larva was taken.

the more coastal waters. Larvae that have shifted into the countercurrents from the South Equatorial Current in the eastern part of its course may well be returned in time for metamorphosis near the coast or at offshore islands. It seems probable, however, that safe return from the area of the more westward stations surveyed is doubtful in view of the great distance covered and the expected attrition through predation, etc. Assuming, as before, that the larvae occurring below about lat. 10°N near long. 120°W, originated in the Galapagos Islands area and allowing an average of 20 nautical miles per day westward flow of the South Equatorial Current it would require 3 mo sustained drift to cover the 1,800 nautical miles involved. If shifted promptly at this point into the North Equatorial Countercurrent with an average speed of 15 nautical miles per day another 4 mo of sustained transport would be required to reach an adult area suitable for metamorphosis. It should be noted, however, that only larval stages VII to XI (final stage) were taken at the more distant stations on all skipjack cruises except *David Starr Jordan* cruise 65, the one nearest to the Galapagos Islands. This would indicate that even the youngest larvae taken near long. 120°W were probably older than 3 mo and the likelihood of much additional delay in returning by way of countercurrents militate against a safe return unless metamorphosis can be delayed pending encountering conditions favorable to metamorphosis and assumption of the benthic habit. Recruitment must depend mainly on larvae that have been retained relatively near the coast by coastwise currents, eddies, and backwashes.

None of the east Pacific larvae taken in the far offshore areas show any tendency to gigantism such as was believed to occur in some Crustacea when settlement has been postponed (Bruce, 1970).

To what extent metamorphosis of the phyllosoma larvae to the postlarval stage may take place in the far offshore waters is not known. No palinurid postlarvae were found in any of the cruises. However, a single specimen of *Scyllarides astori* postlarva (known as a nesto) was taken in a trawl at lat. 01°17′N, long. 120°06′W during *Townsend Cromwell* cruise 51 (Johnson, in press).

The chances of the larvae continuing to float successfully westward all the way to the mid–Pacific islands is unlikely and the absence of the species, except for *P. penicillatus*, in these islands substantiates this supposition and clearly manifests the East Pacific Barrier functioning against westward migration of the east Pacific species.

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REPRODUCTIVE CYCLE OF THE SOFT-SHELL CLAM, *MYA ARENARIA*, AT SKAGIT BAY, WASHINGTON

RUSSELL G. PORTER[1]

ABSTRACT

The annual reproductive cycle of the soft-shell clam, *Mya arenaria* L., was studied at Skagit Bay in northern Puget Sound, Wash. Spawning occurred from late May to early September in both 1971 and 1972 with peak spawning in July and June respectively. Small clams (less than 60 mm in length) had a spawning peak that coincided with other size classes although the spawning period was shorter in duration. The single yearly spawning period at Skagit Bay corresponds with east coast populations in Canada and Maine.

The soft-shell clam, *Mya arenaria* L., is found on virtually all coastlines in the northern hemisphere (Hanks, 1963) and is still extending its range as evidenced by its recent movement into the Black Sea (Zambriborshch, Marchenko, and Telegin, 1968; Ivanov, 1969). On the North American continent, it is native to the east coast from which it reportedly was accidentally introduced into San Francisco Bay, Calif., about 1874 (Fitch, 1953). However, there is some evidence from Indian middens that the soft-shell clam is also native to the west coast (Craig, 1927). Its range on the west coast presently extends from California to Alaska (Morris, 1966).

The reproductive cycle of the soft-shell clam has been described from a variety of locations on the east coast, but no data have been presented for west coast populations except for one brief note from Oregon (Edmondson, 1920). The first detailed study on the histology of the gonad of *Mya arenaria* was conducted by Coe and Turner (1938) in New England. They found that spawning occurred in the summer. At Martha's Vineyard in Massachusetts spawning was found to occur over a 6-mo period from spring through early fall (Deevey, 1948). In northern Massachusetts, spawning occurs in late summer and early fall (Ropes and Stickney, 1965), while in New Jersey, spawning takes place in the spring (Belding, 1930; Nelson and Perkins, 1931). Two spawnings per year (spring and fall) have been reported for the Chesapeake Bay in Maryland (Pfitzenmeyer, 1962, 1965) and for Narragansett Bay, R.I. (Landers, 1954). Ropes and Stickney (1965) have tabulated the results of most east coast studies for easy comparison.

This paper describes the annual reproductive cycle for a soft-shell clam population from Puget Sound, Wash. Skagit Bay was selected as the study area since it has a potential for commercial operations, a commercial soft-shell clam fishery is in the beginning stages, and it appears to be the area with the greatest abundance of soft-shell clams in Puget Sound.

DESCRIPTION OF AREA

Skagit Bay, Wash., is located in northern Puget Sound 60 miles north of Seattle. The Skagit River, which has an average discharge of 16,560 ft^3/s (U.S. Department of Interior, 1971:190),[2] empties into the end of the bay via the South Fork and at the northern entrance of the bay via the North Fork. The northern side of the bay is made up of a large broad mud flat approximately 13 square miles in area. The study area was located on the mud flat off Fir Island between Hall Slough and Browns Slough.

The mean tide range at Skagit Bay is 6.5 feet, and the diurnal range 10 feet. The soft-shell clam beds are located at a tidal level of approximately +3.5 feet.

Water temperatures and salinities in the vicinity of Skagit Bay may vary widely on both an annual and a diurnal basis due to river discharge and tidal effects. During 1971, surface temperatures at Strawberry Point varied from 4.79° to 15.68°C, while salinities ranged from 2.54 to 24.53‰. The maximum recorded daily variation

[1]Washington Cooperative Fishery Unit, University of Washington, Seattle, WA 98195.

[2]Thirty-year period—maximum recorded flow: 144,000 ft^3/s, minimum recorded flow: 2,740 ft^3/s.

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in surface water temperature at Strawberry Point was 4°C.

METHODS AND MATERIALS

The study began in November 1970 and was completed in November 1972. Samples were collected once a month from November thru February and twice a month from April thru October in 1971 and March thru October in 1972. The bimonthly samples were taken at 2-wk intervals: generally during the first and third weeks of the month. No sample was collected in January 1971 because river flooding prevented access to the study area. Each sample consisted of 50 clams which was separated from a larger random sample to represent five size classes: clams less than 60 mm in length, those in the 60–, 70–, and 80–mm length ranges, and those larger than 90 mm. As far as possible the 50 clams selected for each sample were equally distributed between the five size classes. The samples taken during the first 3 mo of the study consisted of only 10, 10, and 15 clams respectively. A total of 1,785 clams were collected which ranged from 22 to 105.5 mm in length. Of this total 2.6% were immature, leaving a total of 1,739 mature clams that were utilized in the analysis of the reproductive cycle.

The samples were returned to the laboratory where they were measured and weighed and the gonadal mass removed and preserved in Davidson's acetic acid fixative (Shaw and Battle, 1957). In smaller clams the entire visceral mass was preserved and sectioned; for larger clams a cube of gonadal tissue was removed from the mid-lateral portion of the visceral mass. Usually dissection and preservation were accomplished the day of collection. Clams not dissected until the following day were held in a refrigerated saltwater system overnight.

Slides were prepared by standard histological techniques: tissues were dehydrated in alcohol, cleared in xylene, embedded in paraffin, sectioned at 5–8 microns, and stained with Mayer's hematoxylin and alcoholic eosin (Galigher and Kozloff, 1971).

The number of gonadal stages used to describe bivalve reproductive cycles varies widely. Lammens (1967) distinguished 11 stages and measured the nuclear-cytoplasmic ratio. Previous investigations on *Mya* reproductive biology generally have recognized five phases of development (Shaw, 1962, 1965; Ropes and Stickney, 1965); therefore the following five phases were used: inactive, active, ripe, spawning, and spent. These five phases were distinguished by the following characteristics.

Males

Inactive (Figure 1a)

During this phase the alveoli are filled with follicle cells which contain the typical male type inclusions as described by Coe and Turner (1938). Primary spermatocytes may be visible along the alveolar wall, but are not abundant.

Active (Figure 1b–d)

This phase is typified by the proliferation and maturing of the spermatocytes. In staging the slides, an early active, middle active, and late active stage were identified. The early active stage (Figure 1b) is characterized by the proliferation of primary spermatocytes at the basal membrane of the alveoli and the appearance of some spermatids. The middle active stage (Figure 1c) is characterized by the disappearance of the follicle cells and the migration of spermatids toward the center of the alveoli where they begin aligning in radial columns. The late active stage (Figure 1d) is characterized by the greatly increased number of radially aligned spermatids and the formation of a central lumen in the alveoli.

Ripe (Figure 1e)

In the ripe male clam, the sperm are distinctly bunched in radial columns around the alveoli with their tails, which stain pink with eosin, projecting into the central lumen.

Spawning (Figures 1f and 2a)

When spawning commences a single row of follicle cells form at the alveolar membrane (Figure 1f). These follicle cells contain the typical inclusions of the male, and the number of rows increases as spawning proceeds (Figure 2a).

Spent (Figure 2b)

In the spent clam most all sperm have been discharged, but a few may remain. The alveoli are almost completely filled with follicle cells.

Females

Inactive (Figure 2c)

In the inactive phase the alveoli are filled with follicle cells which contain the distinctive female

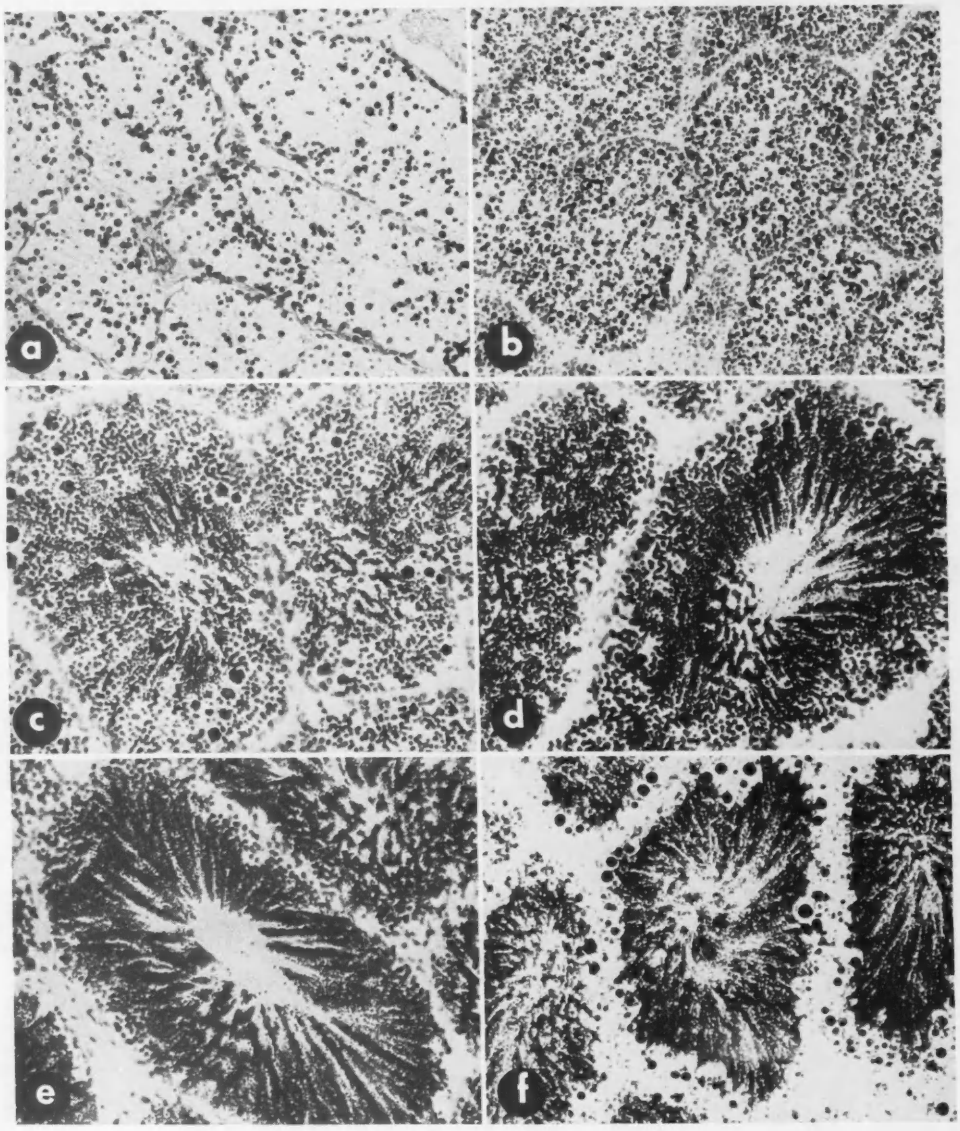

FIGURE 1.—Gonadal stages of the soft-shell clam, *Mya arenaria*, at Skagit Bay, Wash. a) Inactive male (160×), 22 Sept. 1972. Follicle cells with inclusions fill the alveoli. b) Early active male (160×), 17 Feb. 1972. Proliferation of the primary spermatocytes is visible along the basal membrane of the alveoli. c) Active male (250×), 30 Apr. 1971. Spermatids begin aligning in radial columns toward the central lumen of the alveoli. A few sperm balls are visible near the periphery of the alveolus. d) Late active male (250×), 14 May 1971. e) Ripe male (250×), 11 June 1971. The sperm are aligned in radial columns, their tails projecting into the central lumen. f) Early spawning male (250×), 1 June 1972. A single row of follicle cells containing inclusions forms at the basal membrane of the alveoli.

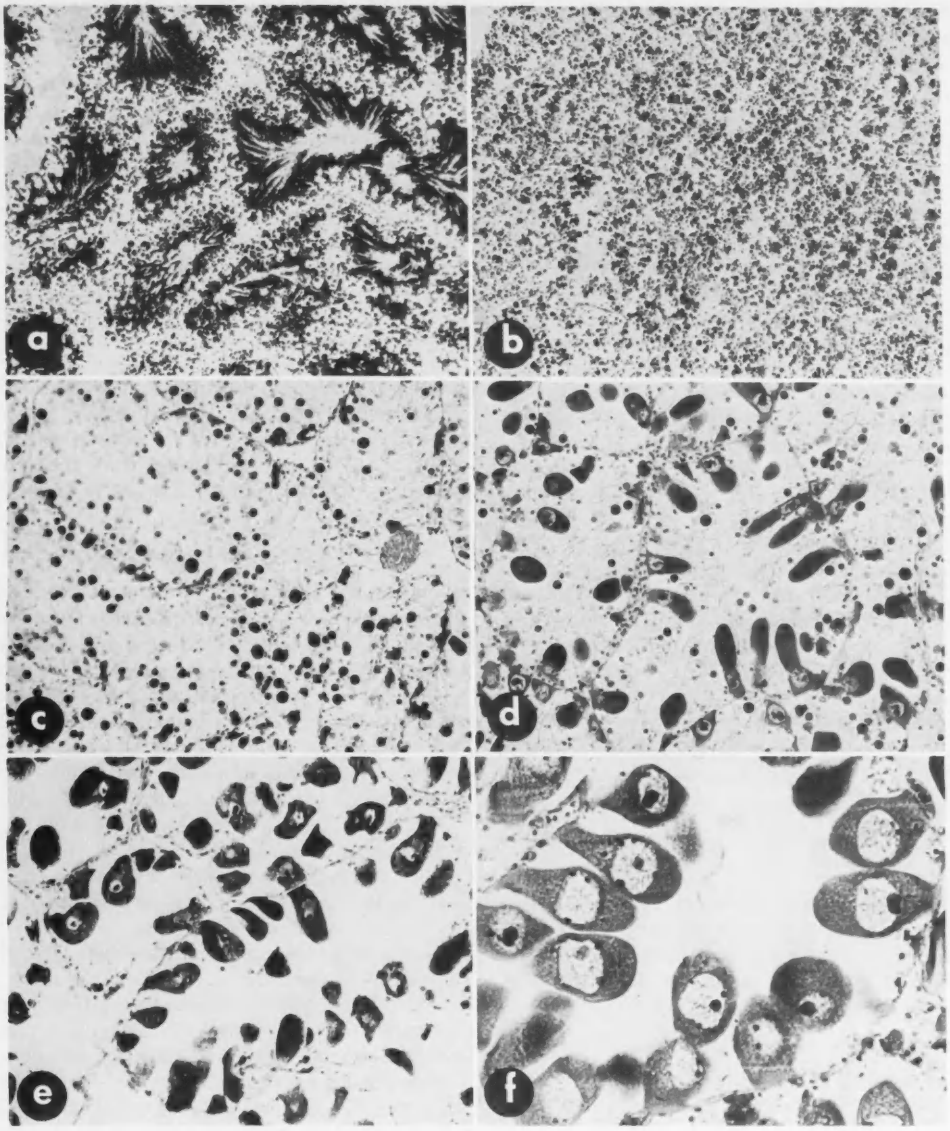

FIGURE 2.—Gonadal stages of the soft-shell clam, *Mya arenaria*, at Skagit Bay, Wash. a) Spawning male (100×), 6 Aug. 1971. The follicle cells reappear as spawning progresses. b) Spent male (100×), 8 Sept. 1972. c) Inactive female (100×), 12 Oct. 1971. Follicle cells containing the typical female inclusions fill the alveoli. d) Early active female (145×), 3 Mar. 1972. The primary ovocytes begin enlarging forming stalked ovocytes. e) Active female (136×), 8 May 1972. The follicle cells and their inclusions have disappeared. f) Late active female (240×), 14 June 1972. The nucleolus and amphinucleolus of the ova have appeared, but most ova are still attached to the basal membrane of the alveoli.

type inclusions (Coe and Turner, 1938). A few primary ovocytes are visible along the alveolar membrane.

Active (Figure 2d–f)

As in the male, three stages were identified for this phase: early, middle, and late active. The early active stage (Figure 2d) is characterized by the proliferation of primary ovocytes and their elongation producing stalks which protrude toward the center of the alveolus between the follicle cells. In the middle active stage (Figure 2e) the follicle cells and their inclusions have disappeared leaving a central lumen in each alveolus. An increasing number of stalked ovocytes attached to the alveolar wall protrude into this lumen. In the late active stage (Figure 2f) the ovocytes are beginning to become spherical with slender stalks, and in many the nucleolus and amphinucleolus are readily visible.

Ripe (Figure 3a, b)

In the ripe phase a majority of the ova are free of the alveolar wall and have taken on spherical shape (Figure 3a). In some individuals the ova are quite abundant, and almost all will be free of the alveolar wall (Figure 3b).

Spawning (Figure 3c)

The spawning phase is characterized by the emptying of the alveoli of ripe ova, leaving behind a few ovocytes that are still attached to the alveolar wall.

Spent (Figure 3d)

In the spent clam the alveoli are empty, and follicle cells begin to fill in the alveoli from the basal membrane inward. Inclusions reappear with the follicle cells, and some of the primary ovocytes are visible.

Immature

The immature gonad (Figure 3e) has a much smaller number of alveoli which are filled with follicle cells devoid of any inclusions.

Each clam was identified as to sex and staged in accordance with the above phases. The percentage of clams in each phase was then calculated. For the purposes of analyzing the reproductive cycle (Figure 4), the three stages of the active phase: early, middle, and late were combined under the single term active phase. In addition, mean monthly percentages were utilized in analyzing the reproductive cycle (Figure 4) for those months during which two samples were collected.

In the presentation of results, the terms 1971 and 1972 reproductive cycle refer to the cycle whose spawning phase occurred during that respective calendar year. However, the reproductive cycle as a whole does not necessarily coincide with, nor is it restricted to, a particular calendar year. The reproductive cycle was assumed to begin with the active phase and end with the inactive phase.

RESULTS

The histological examinations revealed a single yearly spawning period which occurred from late May to early September. This was true for both sexes and for both the 1971 and the 1972 reproductive cycles although the period of peak spawning varied slightly (Figure 4). The sex ratio of the 1,739 clams utilized in the analysis of the reproductive cycle was 48% males (837) and 52% females (902).

1971 Reproductive Cycle

During the 1971 reproductive cycle (Figure 4) clams in the active phase were encountered from February through July for males and February through June for females. Active clams were undoubtedly first present in January although no samples were collected that month. Individuals in the early active stage (Figures 1b and 2d) first appeared in February for both sexes, while those in the middle active stage (Figures 1c and 2e) first appeared in March and the late active stage (Figures 1d and 2f) in early April.

Ripe clams of both sexes were first observed in late April. Ripe males (35%) were most abundant in May and ripe females (47%) in June.

Clams in a spawning condition were first encountered in the later part of May, peaked in July, and were last observed in the early September sample. During July 75% of the males and 55% of the females were in a spawning condition.

Spent clams were present from July to October with the highest percentage occuring in August when 38% of the males and 65% of the females were in this phase.

There was no observed difference in reproductive cycle with size class, except for clams under 60 mm in length. In general the period of peak spawning for those clams was the same as other size classes, but the duration of the spawning period was shorter. It began about 1 mo later than other size classes and ended a month earlier.

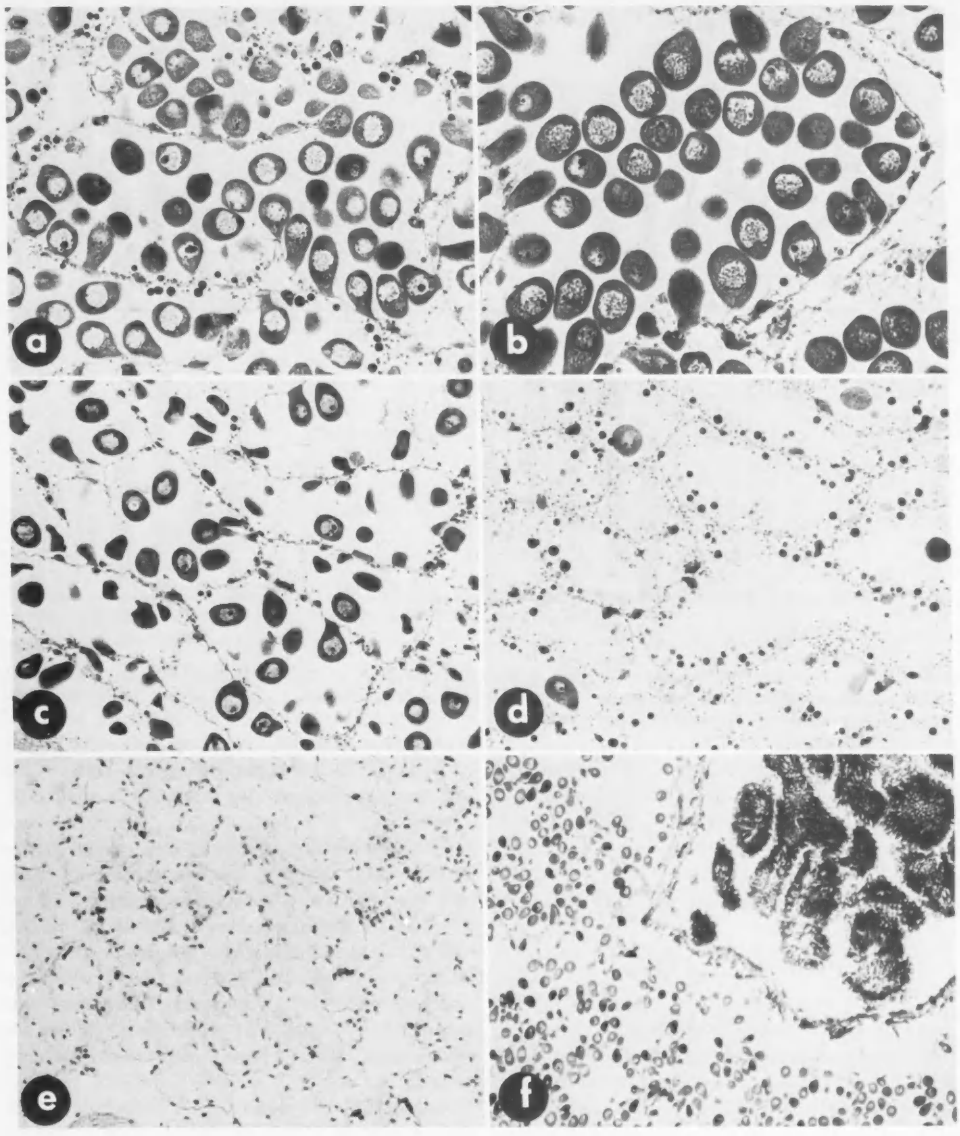

FIGURE 3.—Gonadal stages of the soft-shell clam, *Mya arenaria*, at Skagit Bay, Wash. a) Ripe female (180×), 14 June 1972. The ova are now free of the alveolar wall and have taken on a spherical shape. b) Ripe female (145×), 14 June 1972. c) Spawning female (180×), 1 June 1972. d) Spent female (100×), 24 Aug. 1972. The ova have been discharged, and follicle cells with inclusions are forming along the basal membrane of the alveoli. e) Immature clam (160×), 24 Aug. 1972. Follicle cells devoid of inclusions, but containing the small black follicular nucleii, fill the alveoli. From an individual 38.4 mm in length. f) Hermaphrodite (40×) in a spawning condition (14 June 1972).

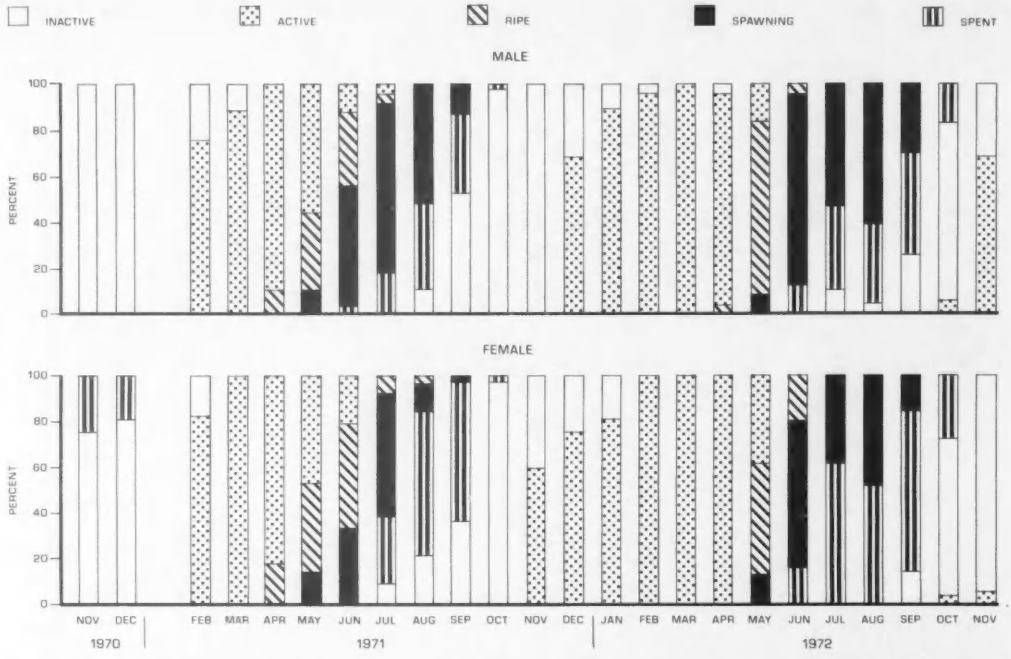

FIGURE 4.—Male and female reproductive cycles of the soft-shell clam, *Mya arenaria*, during 1971 and 1972 from Skagit Bay, Wash. The length of each shaded area represents the percentage frequency of clams in each reproductive phase. A total of 1,739 clams (48% males and 52% females) were examined during the 2-yr study.

The smallest mature male clam examined during the 1971 reproductive cycle was 22.9 mm in length, and the smallest female 31.0 mm. Both were taken in the September sample and were in the inactive phase. The largest immature clam was collected in late May and was 45.2 mm in length.

1972 Reproductive Cycle

The 1972 reproductive cycle (Figure 4) was similar to 1971 with the exception that the cycle as a whole began earlier and the active phase was of longer duration. Active female clams first appeared in November 1971 and active males in December 1971. The active phase lasted until May 1972. During the period from February until April the majority of all clams sampled of both sexes were in the active phase.

Ripe male clams first appeared in April and ripe females in May. Ripe clams of both sexes, 78% of the males and 49% of the females, were most abundant in May.

Spawning commenced in late May and peaked in June for both males (86%) and females (65%) and then continued at a diminished rate until September.

Spent clams of both sexes were present from June through October. They were most abundant in September when 45% of the males and 72% of the females were in the spent phase.

Inactive male clams first appeared in July (10%), while inactive females first appeared in September (13%). The highest percentage of inactive clams occurred in October with 79% of the males and 70% of the females in the inactive phase.

As in 1971, the spawning cycle for most of the clams under 60 mm in length commenced about 1 mo later than the normal cycle and ended 1 mo earlier. The smallest mature clam collected was a 36.3-mm spawning male obtained in July. The smallest mature female was 38.9 mm in length and was in the active phase in March. The largest immature clam was 51.5 mm in length and was collected in March.

In 1971 spawning was quite complete in both

sexes, while in 1972 many of the females failed to spawn completely although the discharge of male sex products seemed complete.

DISCUSSION

The gonadal inclusions of male and female soft-shell clams are distinctive. Coe and Turner (1938) state that the origin of these inclusions is partly from cytoplasmic activity of follicle cells and partly from cytolysis of gametes. The fact that all immature clams in the process of sexual differentiation were found to be developing inclusions characteristic of their sex seems to verify cytoplasmic activity of the follicle cells as one origin of these inclusions. In older male clams, the method of formation of the multinucleated cells first described by Coe and Turner (1938) as pycnotic nucleii and later by Shaw (1965) as sperm balls, needs further study. If the unspawned sperm are retained by the male clam as sperm balls as reported by Shaw (1965) and as my observations indicate (Figure 1c), then perhaps cytoplasmic activity of the follicle cells is the major method by which the inclusions are formed. In female clams the exact relationship between cytolysis of unspawned ova and the formation of inclusions is not known. The single row of follicle cells which form almost immediately at the basal membrane of the alveoli in spent female clams already contain a number of inclusions (Figure 3d) before any of the unspent ova have undergone cytolysis. The origin and function of gonadal inclusions in both sexes requires further investigation.

The gametogenic cycle of the soft-shell clam at Skagit Bay is identical to that reported for clams from the east coast (Coe and Turner, 1938; Shaw, 1962, 1965; Pfitzenmeyer, 1965; Ropes and Stickney, 1965). The single spawning cycle per year, from late May to early September, is similar to that described for studies in eastern Canada (Stafford, 1912; Battle, 1932; Sullivan, 1948) and the New England area (Welch, 1953[3]; Ropes and Stickney, 1965).

The slight variations noted between the spawning cycles of 1971 and 1972 and the incomplete spawning of females in 1972 cannot be explained at present.

Few hermaphroditic *Mya* are reported from other areas (Coe and Turner, 1938; Shaw, 1965). A single hermaphroditic specimen was collected at Skagit Bay (Figure 3f).

[3]Welch, W. R. 1953. Seasonal abundance of bivalve larvae in Robinhood Cove, Maine. Fourth Annual Conference on Clam Research, U.S. Fish and Wildlife Service, Clam Investigations, Boothbay Harbor, Maine, p. 4-6.

ACKNOWLEDGMENTS

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IN SITU EXPERIMENTS WITH COASTAL PELAGIC FISHES TO ESTABLISH DESIGN CRITERIA FOR ELECTRICAL FISH HARVESTING SYSTEMS[1]

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ABSTRACT

In situ experiments to test the efficacy of a scale electrical harvesting system were conducted off Panama City, Fla. with both captured and wild coastal pelagic fishes. Six species of fish were exposed to preselected combinations of pulse rate, pulse width, and voltage by either attracting wild fish or placing captured fish between electrodes. Both captured and wild fish could be effectively controlled with a minimum field strength of 15 V/m, 20 to 35 pulses/s, and a pulse width of more than 0.5 ms. Voltage, pulse width, and pulse rate were equally important for controlling the species tested. Based on these results, resistance measurements were calculated and a potential netless harvesting system specified which would require a minimum energy output of 120 kVA dissipated into an electrode configuration 10 × 5 × 5 m with a load resistance of 0.01558 ohms. The basic design specifications for a prototype pulse generator are provided for netless fish harvesting applications and mid-water trawling.

Commercial fishing for the small, fast-swimming fish schools characterizing much of the pelagic fishery resource in the Gulf of Mexico has been hampered due to a lack in harvesting technology (Bullis and Thompson, 1970). The Southeast Fisheries Center, Pascagoula Laboratory, National Marine Fisheries Service has been engaged in the design and development of an electrical harvesting system capable of economically exploiting this resource. Results from laboratory experiments (Klima, 1972) provided design criteria for a 12-kVA (kilovolt ampere) pulse generator which was used to field test and validate the electrical control parameters and to provide design criteria for a pulse generator capable of commercially harvesting marine fishes from the Gulf of Mexico. This paper describes the results of the electrical in situ experiments using captured and wild fish.

Fishing with electricity was first used in fresh water during the latter part of the 19th century by Ishan Baggs, who was granted a British patent in 1863. Electrical fishing remained in obscurity until after World War I, when McMillan (1928) began to use electricity to systematically guide and lead fish. The use of electrical fishing in the sea has lagged considerably behind that in fresh water because of the high conductivity of salt water, which results in extremely low load resistance and therefore very high current and power requirements for generation of significant field strengths. Kreutzer (1964) showed pulsed direct current could be utilized economically to harvest fish in the sea provided that the field voltage gradient and shape, duration, and rate of impulses are suitable. Electrical stimulation produces either fright, taxis, tetanus, or eventually death, depending upon the electrical field pulse characteristics (Viber, 1967; Halsband, 1967; Lamarque, 1967).

The reaction to various combinations of characteristics varies with species, fish size, and probably other factors (Riedel, 1952; Collins, Volz, and Trefethen, 1954; Bary, 1956; Higman, 1956; Monan and Engstrom, 1963; Kessler, 1965; Halsband, 1967; Klima, 1968); hence, a combination of electrical factors which will induce electrotaxis in one species may induce a fright response or no response in another. As a result, it is critical to know the combination of electrical field characteristics which will produce the desired reaction for each species of interest.

Success of electrical fishing equipment depends upon use of optimum electrical combinations for

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inducing fright, taxis, or even tetanus. These various responses have successfully been used to commercially harvest marine animals. The principal applications include an electrical fish pump for *hardening* menhaden in a purse seine (Kreutzer, 1964), an electrical fish trawl (McRae and French, 1965), and an electrical shrimp trawl (Klima, 1968; Seidel, 1969).

MATERIALS AND METHODS

Test Procedure

Field experiments were performed in the nearshore waters off Panama City, Fla. The test equipment used in evaluating fish response to an electrical field consisted of a deck-mounted pulse generator and an electrode array deployed in the water alongside the vessel. Salinity and temperature ranged from 29.5 to 33.8‰ and 28.0° to 29.6°C, respectively.

Two separate groups of experimental animals were used in the experiments and are referred to as captured fish and wild fish, respectively. The first group consisted of 393 Spanish sardines, *Sardinella anchovia* Valenciennes; 397 round scad, *Decapterus punctatus* (Agassiz); 390 scaled sardines, *Harengula pensacolae* Goode and Bean; 228 Atlantic thread herring, *Opisthonema oglinum* (Lesueur); and 37 Atlantic bumper, *Chloroscombrus chrysurus* (Linneaeus). They were attracted by lights at night and caught with a 5-m lift net in the northern Gulf of Mexico and held in a tank of circulated seawater. Prior to testing, each fish was inspected for damage, and only fish in good condition were used. Each fish was exposed to a preselected combination of pulse rates, voltage, and pulse widths by carefully dropping them into the electrical field facing toward and within 1 m of the negative electrode.

The second group (wild fish) was not handled by the investigators but rather was attracted by lights at night to an area between the electrodes positioned next to the boat. When five or more fish were between the electrodes, they were exposed to preselected combinations of pulse rates, pulse widths, and voltage. Visual observations were used to estimate species composition, approximate size, and responses.

To evaluate the in situ effectiveness of the pulse characteristics tested, we measured the percent of fish which escaped from the electrical field and the percent which swam the length of the field to the positive electrode. The captured fish were introduced into the field in such a way that they were forced to turn 180° in order to swim to the anode, whereas the wild fish schools were randomly oriented. Fish not electrically stimulated when placed between the electrodes exhibited immediate escape movement toward the cathode, the side, or down, but usually did not escape by swimming toward the anode since they were dropped into the electrode array facing the cathode. Test fish would occasionally mill between the electrodes for several seconds before slowly moving away and to the side. Wild fish not electrically stimulated would mill between the electrodes. Consequently, the reactions of the electrically stimulated fish were evaluated in terms of electrotaxis or a positive response by their directed behavior to the anode. We considered swimming to the anode a positive response. All other responses were designated negative.

Description of Test Equipment

The pulse generator providing electrical energy to the electrode array had an output capability of 12 kVA at a pulse rate of 50 pulses/s with a peak output voltage of approximately 150 V at a pulse width of 0.8 ms (millisecond). The pulse rate could be varied from 4 to 55 pulses/s, and three different output widths were available with the unit; 0.3, 0.5, and 0.8 ms measured at the 10% power points. Pulse rise time was around 0.05 ms with a sloped decay. The pulse generator output was designed to operate into load resistance of either 0.05 or 0.2 ohm, since the operational array resistance could not be predicted for all variations in field conditions. At these loads, the output pulse was relatively smooth and undistorted, exhibiting only slight imperfections in the decay portion of the waveform. The waveform was distorted with other array resistances (Figure 1).

In Figure 1D, both the output pulse and the recharging compensating pulse are shown.[3] The compensating pulse is an important feature of the pulse generator and is designed to significantly reduce both electrode electrolysis and electrolysis of any incidental metal within the electrical field, such as a ship's hull. Essentially, the same

[3]Kreutzer, Patent No. 3,363,353; 16 January 1968.

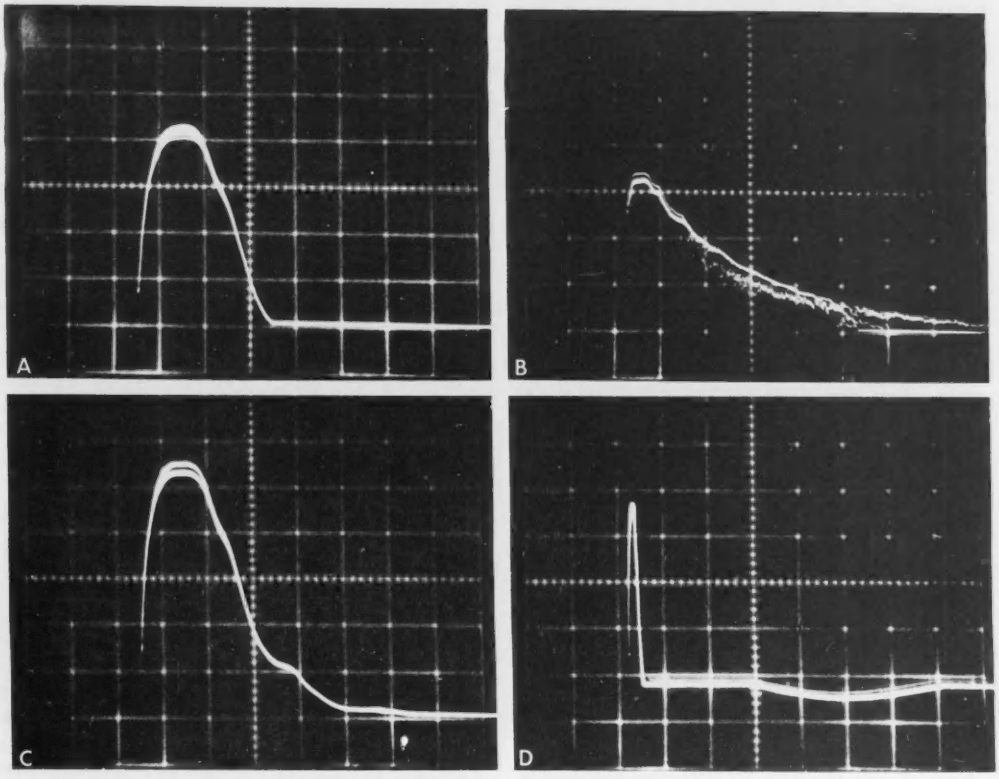

FIGURE 1.—Pulse generator output pulse matched into the load resistance A – low, B – high, C – correctly; the output pulse and compensating pulse are shown in D.

amount of electrical energy is contained within the envelope of the compensating pulse as is within the main pulse except the compensating pulse is of an opposite polarity. The compensating pulse has no effect on fish reaction, since its amplitude is many times less than the main pulse and is below the threshold level of the fish.

The electrode array and pulse generator were designed to effectively energize a minimum volume of water at least 2 m in cross section and 4 m long, and provide a selection of minimum electrical field concentration from 15 to 30 V/m. Each electrode of the array consisted of a copper tube frame with copper strips arranged in a grid pattern. The strips of copper were 15.2 cm wide (6 inches) with square grid openings of 45.7 cm (18 inches) between strips. It has been experimentally demonstrated that the surface of an electrode can be reduced to approximately 10% of the total area and the surface will function electrically as if it were a solid plate (C. Kreutzer,[4] pers. commun.). Our electrode design reduced the conducting surface of the electrode to approximately 53% of the total area. Therefore, this grid technique was utilized to allow the fish to be led to and pass through the anode for easier evaluation of their response. The cable connecting the electrode array to the pulse generator was a 12-m length of 1/0 coaxial conducting cable and represented a total resistance of approximately 0.01 ohm, or a total power loss of 20% in an overall array resistance of 0.05 ohm. Coaxial cable was utilized to eliminate pulse distortion and losses caused by inductance in parallel conductors.

Field strengths listed in volts per meter are averages based on measured electrode-to-electrode values and separation distance between electrodes rather than an in situ field strength

[4]Smith Research and Development Company, Lewes, Del.

measurement, because the density of an electrical field in seawater is not uniform. For ease of measurement, the electrode-to-electrode voltage was measured at the output of the pulse generator and did not take into account cable and connection losses. Also, due to the hookup restriction in the research vessel's instrumentation room, short lengths of parallel conductors were utilized, resulting in a 40% total cable loss. Therefore the true electrode-to-electrode voltages and average field strengths are related to measured values as follows:

A. 150 V = 90 V electrode to electrode = 22.5 V/m.
B. 120 V = 72 V electrode to electrode = 18.0 V/m.
C. 90 V = 54 V electrode to electrode = 13.5 V/m.
D. 60 V = 36 V electrode to electrode = 9.0 V/m.

The configuration of the electrical field at a pulse generator output of 120 V along with actual measured field strengths (expressed as voltage drops measured across 10 cm) at various positions within the field are shown in Figure 2A. The measurements are fairly close in value but not exact. The pickup probe was attached to a long pole and the measurements taken from the side of the RV *George M. Bowers*. Because of water current and boat movement, it was difficult to hold the probe parallel to the electric field in exactly each position shown.

Laboratory tests indicated a field strength of about 15 V/m was required to properly produce electrotaxis in fish 10 cm long. Field strengths throughout the volume of water within the electrode envelope could be maintained equal to or greater than the 15 V/m requirement.

Based on initial field tests, the general zones of fish response produced by the electrode array are 1) effective control, 2) possible control, depending on fish size and its orientation, and 3) fright zone (Figure 2B). The zone of control also extends to the back side of the positive electrode.

RESULTS

Captured Fish

Voltage, pulse width, and rate are equally important for controlling the species tested (Figures 3–5, Table 1). Comparison between the pulse widths indicates that a higher percentage of experimental animals were controlled at the wider pulse widths (0.8 ms). The lower and intermediate stimulation voltages (60 and 90 V) were not as effective in controlling the animals as the higher voltage (120 V). Furthermore, the combination of 0.8 ms pulse width with 120 V appeared to be adequate for inducing electrotaxis at the widest range of pulse rates (20 to 35/s).

The ideal pulse rates for inducing electrotaxis varied for each species. Spanish sardines and scaled sardines were under good control at 20 to 35 pulses/s and round scad at 25 to 35

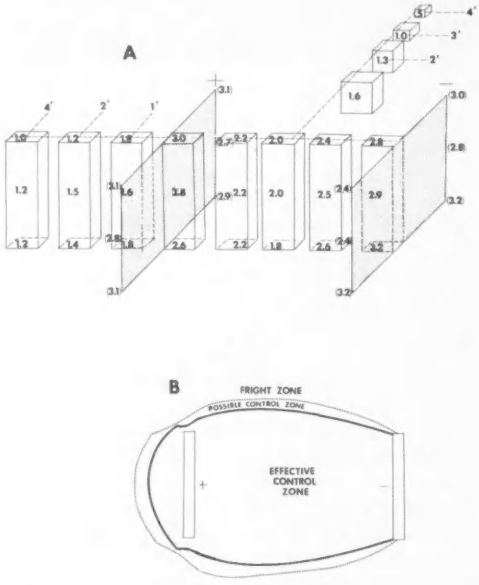

FIGURE 2.—A. Field strength configuration at 72 V electrode to electrode. B. General zones of fish response.

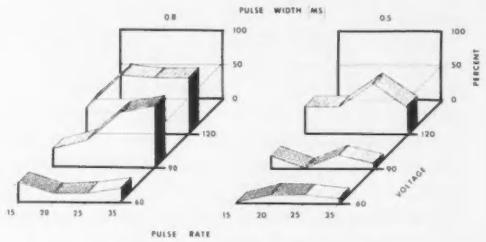

FIGURE 3.—Percent positive response of scaled sardines to various combinations of voltage, pulse rate, and pulse width.

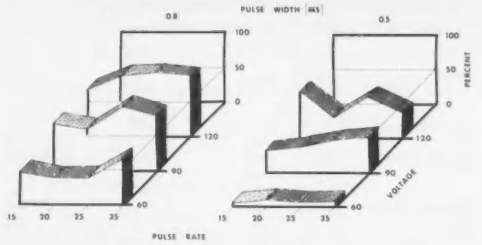

FIGURE 4.—Percent positive response of Spanish sardines to various combinations of voltage, pulse rate, and pulse width.

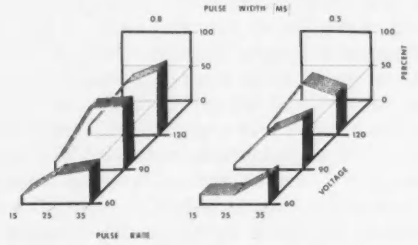

FIGURE 5.—Percent positive response of round scad to various combinations of voltage, pulse rate, and pulse width.

TABLE 1.—Percent of thread herring and bumpers at various stimulation parameters. Each observation consisted of 15 individuals except where noted.

Voltage and pulse width	Pulse rate			
	Thread herring			Bumper
	15	25	35	25
60 V; 0.5 ms	56	53		[1]50
90 V:				
0.3 ms	20	67		
0.5 ms	[2]61	63		80
0.8 ms		100	85	
120 V:				
0.3 ms	27	47		
0.8 ms	41	67		75
150 V; 0.3 ms	33	53	73	

[1]7 individuals.
[2]31 individuals.

pulses/s. Based on the limited data for thread herring and bumper, the best pulse rates were 25 to 35 pulses/s.

A factorial analysis was used to determine the most effective combination of pulse rate, width, and voltage for controlling Spanish sardines, scaled sardines, and round scad (Table 2). This analysis demonstrates that selection of the proper level of voltage, pulse width, and pulse rate are clearly important for controlling these species. Another important aspect may be the interactions between the three main effects, although the meaning behind this significance is uncertain. It can be seen from Table 2 that these interactions vary between species. Interdependence was observed for all tested electrical combinations in scaled sardines and Spanish sardines. Surprisingly, this was not observed for the round scad. Voltage and pulse rate interact for scaled sardines and round scad.

General observations for the first (captured) group of fish indicated if the electrical combination was not adequate, these fish would immediately escape to the side or towards the cathode. However, at times when the pulse width was 0.3 ms, thread herring would elicit a jump and skip on the surface of the water and dart out of the field. This escape behavior was never observed at the wider pulse widths. Controlled fish would swim to the anode and circle between the plates of the electrode from the inside of the field to the back of the field and back again in a circular swimming motion, and were held until the power was turned off.

The most effective electrical combinations for each species are listed in Table 3. We felt that if 70% or more of the experimental group responded positively, the combination was effective. Output voltages of 60 V or less were ineffective for controlling fish regardless of the pulse rate or pulse width. Effective fish control required an output voltage of at least 90 V with a pulse rate of 25 or more, and except for bumper the pulse width had to be 0.8 ms. An overall effective electrical combination was 120 V at 25 to 35 pulses/s at 0.5 to 0.8 ms, and 90 V at 25 to 35 pulses/s at 0.8 ms.

Wild Fish

The second group of fish was attracted into the electrode configuration by a surface nightlight positioned above the electrodes and then stimulated. Usually we were successful in attracting sufficient quantities of fish to evaluate a specific combination of electrical parameters. However, their exact position between the electrodes was never the same, especially when a large school of 30 to 50 fish were positioned between the electrodes. We only used electrical field characteristics which appeared to be successful during our daytime experiments with individual captured

TABLE 2.—Multivariant analysis of variance to determine which parameters are most useful to control Spanish sardine, scaled sardine, and round scad with probability levels (* significant at $P = 0.15$; ** significant at $P = 0.05$).

Source of variation	Spanish sardine				Scaled sardine				Round scad			
	Degrees of freedom	Mean square	F	Level of significance	Degrees of freedom	Mean square	F	Level of significance	Degrees of freedom	Mean square	F	Level of significance
Voltage	2	6,172.8	24.92	0.001**	2	8,827.1	36.25	0.001**	2	3,970.5	34.83	0.001**
Pulse width	1	17,328.0	69.95	0.001**	1	8,938.0	36.71	0.001**	1	2,809.0	24.64	0.001**
Pulse rate	3	578.1	2.33	0.099*	3	1,263.7	5.19	0.007**	2	8,149.5	71.49	0.001**
Voltage/pulse width	2	15.8	0.06	0.939	2	1,508.8	6.19	0.007**	2	110.6	0.97	0.398
Voltage/pulse rate	6	360.2	1.45	0.236	6	491.3	2.02	0.103*	4	633.1	5.55	0.004**
Pulse width/pulse rate	3	104.3	0.42	0.740	3	574.9	2.36	0.097*	2	50.6	0.44	0.648
Voltage/pulse width/pulse rate	6	496.5	2.00	0.105*	6	494.6	2.03	0.101*	4	435.7	3.82	0.020
Error	24	247.7			24	243.5			18	114.0		

TABLE 3.—Effective electrical combinations based on a minimum of 70% eliciting a positive response (Group 1 fish).

Species	Volts	Pulse rates	Pulse width
Spanish sardine	90	25-35	0.8
	120	20-35	0.8
Round scad	90	25-35	0.8
	120	25	0.5
	120	25-35	0.8
Scaled sardine	90	25-35	0.8
	120	25	0.5
	120	20-35	0.8
Thread herring	90	25-35	0.8
Bumper	90	25	0.5
	120	25	0.5

fish. The wild fish were only exposed to a pulse width of 0.5 ms, as the time between tests did not permit a change in pulse width. Since this pulse width provided satisfactory results, we felt that either 0.5 or 0.8 ms would be satisfactory, as indicated from our captured fish experiments. Visual observations indicated that the larger fish (>10 cm) reacted more quickly and swam to and from the anode before the smaller fish (<10 cm) did. Table 4 provides details and summaries of our nighttime observations with wild fish. In general, Spanish sardines and round scad were controlled adequately at 120 V and a pulse rate of 25 to 35 pulses/s at a pulse width of 0.5 ms. When large schools were attracted between the electrodes, it was not always possible to control all of the animals. Our visual observations indicated that fish in the fringe area would escape since the voltage gradient was insufficient to control fish in the fringe areas. The number of fish escaping probably varied with their position in the electrical field and their size, since smaller fish require higher voltage gradients for control than large fish. At 35 pulses/s and 120 V, we were able to pull or force fish into the electrode array from the back side of the positive electrode. Positive reactions were elicited in all species at the prime voltage of 120 and pulse rates between 25 and 35. The results from the wild fish experiment conclusively demonstrate that coastal pelagic fish of the species tested can be controlled and led with combinations of 120 V, 25 to 35 pulses/s, and a pulse width of 0.5 ms.

DISCUSSION

Effective electrical combinations for controlling coastal pelagic species determined during our field experiments compared favorably with the parameters determined by Klima (1970) in labora-

TABLE 4.—Responses of wild fish attracted to electrode configuration at preselected electrical combinations (pulse width — 0.5 millisecond).

Species	Approximate school size	Volts	Pulse rate	Reactions
Spanish sardine, round scad and bumper	10-15	120	25	Positive; pulled into anode and held.
Spanish sardine, round scad and bumper	10-15	120	35	Positive; pulled into anode and held.
Spanish sardine and round scad	30-50	120	35	Positive 50 to 90% led to anode and held; only fish in fringe area escaped.
Thread herring and bumper	5-8	120	35	Positive; led to anode.
Spanish sardine	10	90	15	3 had positive response.
Spanish sardine and round scad	10	100	50	Turn fish to anode—all escaped.
Spanish sardine and round scad	10	100	25	Turn fish to anode—all escaped.
Round scad	20-40	120	35	Positive and held at electrode.
Blue runner, *Caranx crysos*	15	120	25	Positive and held at anode.
Blue runner	10	120	35	Positive and held at anode.
Blue runner	30	120	35	20-25 positive response and held at anode.

tory studies. The range of pulse widths was slightly narrower in the field than in the laboratory where the experiment tank maintained a uniform field, test animals could not escape, and in which narrow pulse widths were not possible. Since wide pulse widths require more electrical energy, it is desirable to select the narrowest pulse width possible which will allow proper control of the species. This in situ investigation clearly demonstrates that pulse widths between 0.5 and 0.8 ms can be effectively employed in open water situations in conjunction with proper field strengths and pulse rates. Our results demonstrate that the effective control of the fishes tested requires no less than 15 V/m at pulse widths of 0.5 ms or greater and pulse rates ranging between 20 and 35/s. A pulse width of 0.3 ms was completely ineffective within the proper field strength and pulse rate range used in our experiment.

A review of the field test data suggests an additional parameter, minimum pulse control power for a specific pulse width and field strength, should be determined during future field experiments. Obviously a minimum output voltage and current is necessary to maintain the established 15 V/m in any particular electrode configuration and resulting load resistance. However, once the minimum power to maintain 15 V/m is reached, if future research can establish that a pulse envelope of minimum total power within a minimum and maximum set of values for pulse rate and pulse width is the important criterion for proper fish control, much greater latitude would be possible in designing a pulse generator for a particular fishing system. This would permit a designer to better select pulse rate, pulse width, and maximum values for voltage and current to provide better equipment reliability and possibly cheaper construction.

The power required to control fish is presented in the following discussion based on the parameters of pulse width, pulse rate, and field strength which we used as criteria during the field tests. Power for each pulse (P_p) is described as:

$$P_p = V_e \times I \times P_w \qquad (1)$$

where V_e = electrode voltage
I = current at load resistance in amperes
P_w = pulse width, milliseconds.

The total load resistance equaled 0.05 ohm with an electrode-to-electrode resistance of 0.033 ohm and a cable loss of 0.017 ohm. Slight daily variations of 0.006 ohm were noted in electrode-to-electrode resistance due to small changes in salinity and temperature. For computations, we rounded the resistance values slightly and the electrode-to-electrode voltage was established as 60% of the output voltage. The current (I) and electrode-to-electrode voltage (V_e) at selected output voltages using an array resistance of 0.03 ohm and a loss resistance of 0.02 ohm were:

Output voltage	V_e	I
150	90	3,000
120	72	2,400
90	54	1,800

The total power (kW) delivered into the electrode array after cable losses can be computed as follows:

$$P_t = V_e \times I \times P_w \times P_r \qquad (2)$$

where P_r = pulse rate, pulses per second
P_t = total power in kilovolt ampere.

Using the above values, the total power for effective electrical control values used was:

V_e	P_r	P_w	P_t
54	25	0.8	1.94
72	25	0.5	2.16
72	25	0.8	2.77
90	35	0.3	2.84

The preceding results suggest there is a minimum requirement of total power (P_t) to properly control the fish which would be a constant regardless of the specific combinations of pulse width, pulse rate, and field strengths. Once the effective field strength of 15 V/m is exceeded, it appears that different minimum values of pulse rate and pulse width can be obtained to produce equally effective fish response. Unfortunately, there are too few data points to support this conclusion. To properly substantiate such a hypothesis, we would have to determine either a minimum pulse width for a constant electrode voltage at each pulse rate or a minimum pulse rate for a constant electrode voltage at each pulse width. Without this, we cannot definitely state that a parameter of total power (P_t) can be used as a control specification rather than various combinations of electrode voltage, pulse width, and pulse rate. Many more tests would be needed to substantiate the hypothesis, although this approach would be advantageous from a designer's standpoint.

120-kVA Pulse Generator Design

The primary objective in the design of our pulse generator was to produce a system which, based on the results of the 12-kVA pulse generator electrical fish control experiments, would provide the capability for prototype development and effective harvest of fish in several modes of system operation. The output power of the pulse generator and pulse control characteristics were established to satisfy requirements for automatic fish harvesting without nets (Klima, 1970), electrical mid-water and bottom trawling for fish, and to provide the potential for prototype development of possible future applications such as fish barriers, electrical aquaculture cages, or other such applications.

Netless Fish Harvesting Mode

The initial reason for our development efforts in the field of electrical fishing was to eventually achieve the automatic fish harvesting system. Since this application imposed the most serious power demands, the design specifics were established around that set of conditions and results of this study were used to calculate the power requirements for a netless fishing system. Allowances were made, however, for application of the system to other electrical control applications. One, a mid-water trawl mode, is described later in the paper.

Use of lights at night concentrate fish (Wickham, 1971) in a volume of water which can then be electrified. The minimum volume of water within a light field which needs to be effectively covered electrically to produce commercial quantities of fish would be 5 m in cross section and 10 m in length. An equation for resistance of seawater between the electrodes is:

$$R = \frac{\rho L}{A} \qquad (3)$$

where L = distance between electrodes in meters
A = surface area of the electrodes in square meters
ρ = resistivity of seawater in ohm-meters.

According to this equation the load resistance of two parallel plates is:

$$R = \frac{0.213 \times 10}{25} = 0.0852 \text{ ohm}$$

where ρ at $30^0/_{00}$ and 24°C = 0.213 ohm-m.

However, this formula only describes the resistance of the volume of water between two electrodes as if the electrode array was a finite conductor. In actual practice, a significant spreading of the electrical field occurs in seawater. If the size of an electrode is small in comparison to the

separation distance, the configuration of the electrode in the array is the principal factor in determining the resistance value, as would be the case with small balls or cables for electrodes. For our situation, the size of the electrodes and separation distance are equally important. Since the load resistance of the array in seawater is extremely low, the resistance value used to calculate power requirements becomes extremely important. A small error in the resistance could result in a large miscalculation of the necessary power requirements. For this reason we took great care in computing resistance accurately. Resistance measurements for this situation can be calculated by two methods referred to as Kreutzer and empirical technique. Kreutzer developed a formula for calculating spread resistance for one electrode:

$$R_s = \frac{K_o (1 + T \times 0.02)}{\sqrt{A}} \qquad (4)$$

where R_s = spread resistance of one electrode, including field fringing
K_o = a constant at a specific salinity
T = temperature in centigrade
A = area, square meters.

(C. Kreutzer, pers. commun.) The constant K_o varies with different salinity values and must be recalculated for each new salinity. It can be obtained by solving for K_o in Equation (4) which requires knowledge of resistance, surface area, and temperature. Once the value of K_o is determined for a specific salinity, Equation (4) can be used to calculate R_s for varying electrode surface areas. Because the value of K_o varies with different salinity and is difficult to determine since in situ resistance measurements are required, we decided to establish an empirical ratio which compares the theoretical calculated resistance from Equation (3) to an actual measured electrode resistance. The calculated resistance according to Equation (3), using the 2 × 2 × 4 m electrodes of one test was:

$$R = \frac{0.189 \times 4}{4} = 0.189 \text{ ohm}$$

with a salinity of 32.9‰ and a temperature of 28.7°C (ρ = 0.189 ohm-m). The measured resistance was actually 0.039 ohm. An index of difference between the calculated and measured resistance provides a ratio of 4.85. The ratio of calculated to measured resistance ranged from 4.85 to 5.2 throughout the study period, with the measured resistance of the electrode array varying from 0.035 to 0.04 ohm. Hence, a midrange value of 5.0 seems the most practical and resistance value one-fifth of the Equation (3) calculated value is used to compute total spread resistance as shown in the following equation:

$$R_t = \frac{\rho L}{5A} \qquad (5)$$

where R_t = total spread resistance including both electrodes.

As a cross-check to Equation (5) we also computed the spread resistance from Equation (4) using a value of K_o derived from the sample test. The measured resistance of the electrode array in seawater was 0.039 ohm. Since each electrode contributes one-half the resistance, the spread resistance for Equation (4) is 0.0195 ohm. In addition, since both sides of each electrode in our tests were exposed, the surface area for the equation is twice that of one side. Using these values, K_o is determined to be:

$$0.0195 = \frac{K_o (1 + 28.7 \times 0.02)}{\sqrt{2(2)^2}}$$

where K_o = 0.035 ohm-m.

For a 5 × 5 × 10 m electrode array using Equations (4) and (5), the following load resistances are determined at 28.7°C and 32.9‰:

Equation (4)

$$R_t = \frac{0.189 \times 10}{5(5)^2} = 0.01512 \text{ ohm},$$

Equation (5)

$$R_s = \frac{0.035 (1 + 28.7 \times 0.02)}{\sqrt{2(5)^2}} = 0.00779,$$

where R_t = $2R_s$ = 2(0.00779) = 0.01558,
R_t = $2R_s$ since R_s is the resistance of one electrode.

As can be seen, the value for the load resistance of a 5-square meter by 10-m array compares favorably when determined by the two different equations. The higher value of 0.01558 ohm was used in making power calculations since any electrode array will have some additional resistance due to connection losses.

Results from our field study thus provided the following set of basic design specifics for our prototype pulse generator for use with attracting lights in a netless fish harvesting application:

1. Minimum field strength – 15 V/m.
2. Pulse rate – 20-35 pulses/s.
3. Pulse width – $\geq$0.5 ms.
4. Array size – 5 × 5 × 10 m.
5. Load resistance of array – 0.01558 ohm.

Using these specifications, we determined the output capability of the pulse generator which would satisfy our requirements by the following equation:

$$P = VI \times fl \qquad (6)$$

where P = power, watts
V = output voltage, volts
I = current, amperes
f = pulse rate, pulses per second
l = pulse length or width, seconds.

To insure an adequate field strength throughout our electrode array, we chose a value of 20 V/m for the power calculations. We also selected a maximum pulse rate of 50/s and pulse widths of 0.5, 0.75, and 1.0 ms to give the pulse generator more versatility. Using Equation (6), the power requirement is:

$$V = 20 \times 10 = 200 \text{ V for 10-m array}$$

$$I = \frac{V}{R_t} = \frac{200}{0.01558} = 12{,}837 \text{ A},$$

and at 50 pulses/s and 0.75 ms pulse width

$$P = (200)(12{,}837)(50)(0.75 \times 10^{-3})$$
$$P = 96{,}278 \text{ W}.$$

In an applied system, a cable and connection loss will be experienced. Because of the very low load resistances of seawater, a 25% cable loss can easily be expected. Rounding off our requirement to 90 kVA and after allowing for a 25% loss, we need a pulse generator of 120-kVA output to satisfy the system requirements we established.

As a crosscheck of the above designed system, the following formula (Kreutzer, 1964) is used to calculate the effective fish control range of one electrode:

$$R = \sqrt{\frac{I \times L \times \rho}{G \times 2 \times \pi}}$$

where R = effective range, meters
I = current into the water, amperes
L = length of fish, meters
ρ = water resistivity, ohm-meter
G = body voltage of fish.

To determine the effective range of 20 V/m, a value of 1 m is used for the fish length, fish body voltage is 20 V, and the resistivity is again 0.189 ohm-m.

Allowing a 25% cable loss requires a total input voltage of 267 V at a total load resistance of 0.0208 ohm, and the current in the water is found to be:

$$I = \frac{V}{R} = \frac{267}{0.0208} = 12{,}837 \text{ A}.$$

Using these values, range (R) is found to be:

$$R = \sqrt{\frac{12{,}837 \times 1 \times 0.189}{20 \times 2 \times 3.14}}$$
$$R = 4.40 \text{ m}.$$

Since this value is computed for one electrode, the 20 V/m range of two electrodes will be 8.8 m. In actual practice, however, the range of two electrodes paired together is greater than twice the reach of one, and we can supply a 5 × 5 × 10 m array with 20 V/m. At our minimum specification of 15 V/m, the calculated reach of one electrode is 5.08 m.

Since the configuration of the electrode array determines array resistance, various combinations of electrode size and separation distance can change the pulse voltage and current requirements. For this reason, a certain degree of flexibility was designed into the netless fish harvesting mode of the pulse generator. The system is

capable of delivering up to 1,000 V to an electrode array. However, at this voltage, the array shape has to be changed to produce a much higher load resistance to maintain the current at a value which is within the 120-kVA rating of the system and the current and voltage carrying capability of various components in the unit. For instance, at 1,000 V the electrode array has to have a total resistance of 0.3 ohm.

Mid-Water Trawling Mode

The pulse generator was also designed for application to electrical trawling. This use of the system requires a significantly different configuration than in netless harvesting. Since the pulse generator components are far too large to consider underwater mounting of the system on a trawl, it was necessary to design the unit for operation through a long power cable. The cable transmits the pulsed power from the vessel to the trawl. A cable length of 2,200 feet (670.1 m) was chosen to allow trawling to depths of 100 fm (fathoms) (182.9 m) with a cable to depth ratio of at least 3:1. The length of the cable is important because as it gets longer its direct current resistance increases and therefore either the cable losses become greater or the size of the conductors has to be increased to prevent excessive losses. Since a large power loss is not acceptable, conductor size and the resulting cable diameter eventually become too large and are limiting factors in the total length and therefore the power then can be transmitted down the cable.

The operation of a pulse generator into a long cable requires careful design in order to work. First, the impedences of the pulse generator, cable, and electrode array have to be properly matched through step-up and step-down transformers to accomplish transmission of the pulse down the cable. Unless impedences are properly matched, the pulse will become very distorted or can be totally lost in the cable. Another serious limiting factor in the operation of a pulse generator through a long cable for trawling is the underwater transformers which match the power supply cable to the electrode array. The delivery of significant levels of power, such as 120 kVA, through a single transformer would require a transformer that is quite large and would weigh several hundred pounds to handle the pulse current into an array with a load resistance of 0.05 ohm.

Our first intended application of the pulse generator in a trawling mode was with a mid-water trawl. The standard mid-water trawl being used at the Pascagoula Laboratory was a net that opened approximately 9 × 9 m under water. In actual field measurements, it has been found that the net generally opens between 7.5 and 9.0 m in height. Therefore we required the pulse generator to accomplish effective electrical trawling on a vertical opening of 7.5 to 9.0 m and a horizontal opening of approximately 9.0 m. In the mid-water trawl application we expect the electricity to provide a combination of fright, leading, and some tetanus to aid in harvesting of fish. Past experiments at the Pascagoula Laboratory demonstrated that fish generally accumulate in the mouth and forward body of the trawl. Therefore an electrical field applied periodically should force the fish back into the cod end.

Because of component ratings, loading of underwater transformers, and design restrictions, a power of 80 kVA was chosen as the maximum which could be supplied to our electrode array in a mid-water trawling mode. Since the application of 80 kVA through a single transformer is difficult under water, we chose four electrode pairs and four underwater transformers matched to each electrode pair to cover the 9.0 × 9.0 m net. It was found that a reasonable electrode size could be used which would provide a load resistance of 0.2 ohm for each pair and deliver 20 kVA from each transformer. This meant that by connecting the electrode pairs in parallel, each transformer would carry one fourth the current which would be required of a single transformer at the same total output. In addition, the four parallel electrode pairs would represent a total load resistance of 0.05 ohm which could easily be matched to the other impedences of the system.

Within the impedence matching requirements of the pulse generator, cable, and electrode array, and using the maximum output voltage of 2,500 V that the unit is capable of supplying in this mode, 450 V can be supplied to each electrode pair through the matching transformers. The surface area of each electrode pair must be adjusted to provide a resistance value of 0.2 ohm. Therefore, the pulse current of this condition is:

$$I = \frac{V}{R} = \frac{450}{0.2} = 2{,}250 \text{ A.}$$

Using Equation (7) at 15 V/m, the range of an electrode is:

$$R = \sqrt{\frac{2{,}250 \times 1 \times 0.189}{15 \times 2 \times 3.14}}$$

$$R = 2.13 \text{ m.}$$

However, to accomplish at least a fright reaction required 10 V/m or less, depending on fish size. We feel that a fright reaction, although not as effective as positive control of fish, will accomplish disorientation and therefore harvest of some fish in an electrical trawling mode. Since the temperature of below-surface water will be colder, we can use higher resistivities than 0.189 in calculations as shown in the following calculation for field reach at 100 fm water depth. In addition, Kreutzer's Equation (7) states that the factor in the denominator goes from 2 to 4 as the electrodes are placed in mid-water. Using these values, we calculate the maximum variation of values from the surface to 100 fm in the 10 V/m range of one electrode to be:

Surface:

Salinity 32.9‰, temperature 28.7°C, $\rho = 0.189$

$$R = \sqrt{\frac{2{,}250 \times 1 \times 0.189}{10 \times 2 \times 3.14}}$$

$$R = 2.60 \text{ m.}$$

100 fm:

Salinity 30‰, temperature 10°C, $\rho = 0.3$

$$R = \sqrt{\frac{2{,}250 \times 1 \times 0.3}{10 \times 4 \times 3.14}}$$

$$R = 2.32 \text{ m.}$$

Again, the range of two electrodes is found to be greater than twice the range of one electrode. In addition, since each electrode pair based on their required size for 0.2 ohm, will be separated by about 1.22 m, field strength adding will occur. Therefore, the effective range of an electrode pair is significantly more than twice the range of one electrode. By installing one polarity electrode on the headrope and the opposite on the footrope, we should be able to cover a 9 × 9 m area with the weakest part of the field having at least enough strength to frighten fish. We can also use pulse rates higher than 35/s, which will immobilize fish more rapidly. In addition, it must be remembered that at distances closer to the electrodes, the field strength increases and reaches values which will effectively lead or stun the fish. Because the size of each electrode is relatively small, current densities capable of stunning fish will be found at some minimum distance from the electrodes. This is not desirable for leading fish in a netless harvesting application and is avoided by using large electrodes, but it is very desirable in a trawling mode where the electrodes are inside the body of the net.

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ECOLOGY AND NATURAL HISTORY OF A STAND OF GIANT KELP, *MACROCYSTIS PYRIFERA*, OFF DEL MAR, CALIFORNIA

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ABSTRACT

The assemblage of plants and animals living within a stand of *Macrocystis pyrifera* off the coast of southern California was studied from July 1967 through February 1973. *Macrocystis* is a perennial kelp, with some individuals living as long as 7 yr; however, the average life span in this bed was approximately 3 to 4 yr. Physical disturbances associated with storms were the major mortality causes of adult *Macrocystis* in this area. Once detached, these plants drift through the bed and become entangled with other plants which results in extensive mortality. The fact that germination was greatest after the surface canopy was thinned by natural attrition and commercial harvesting suggests that light is a critical factor influencing the recruitment of *Macrocystis*. There was little indication to show that sea urchin grazing contributed to kelp mortality.

Faunal species identified included 38 fish species and 98 invertebrate species. Of these, 14 species of macroinvertebrates were chosen for more intensive study as they represented common or characteristic species in the kelp bed. Patterns of distribution and abundance were recorded during the study period. Most species had aggregated distribution patterns and the populations of most remained reasonably constant over 4.25 yr. *Styela montereyensis* (ascidian) fluctuated annually and the *Muricea californica* (octocoral) population slowly decreased during this time. Conversely, *Diopatra ornata* (polychaete) displayed a numerical increase, such that in August 1972 it was the most abundant macroinvertebrate in the Del Mar kelp bed. A qualitative food web is presented based on limited trophic information.

Many large kelp stands historically have either undergone dramatic oscillations in areal cover and standing crop or completely disappeared (see North, 1971, for history and data). Nearshore kelp stands are found in many scattered locations along the mainland of California and fringe most of the state's offshore islands; in southern California kelps are often conspicuous when the dominant plant, *Macrocystis pyrifera* (Linnaeus) C. Agardh, forms a floating canopy or bed along the sea surface. This kelp community contains many plant and animal species which contribute aesthetic as well as diverse recreational and commercial resources. The loss and deterioration of these stands is correlated with many man-caused perturbations and natural events such as reduced water quality, the over-harvest of numerous important component animal populations, and fluctuations in seawater temperature.

There is widespread concern regarding effects of increasing human perturbations to these nearshore kelp communities which include increasing recreational and commercial usage as well as many projected sewer and thermal outfalls into or in the proximity of kelp beds. Despite this concern, there is little information regarding natural temporal variation of populations inhabiting these assemblages. Furthermore, natural history data such as food web interactions critical to a functional understanding of this community are in a very rudimentary state. This information is obviously vital to the proper management of this resource.

The objectives of this paper are to: 1) describe patterns of distribution and abundance, 2) record long term population fluxes, and 3) note food web and other natural history observations of conspicuous members of a relatively undisturbed kelp association. Such data are essential to the growth of a functional understanding of this community.

The study site (Figure 1) was located in a bed of *Macrocystis pyrifera* about 1 km offshore from Del Mar, Calif. (lat. 32°57'N, long. 117°16'W). The majority of the observations were made at

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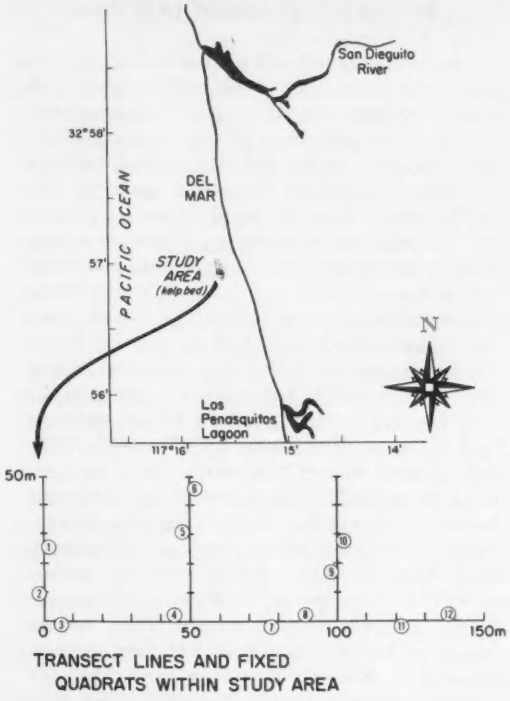

FIGURE 1.—Location of the subtidal study area off Del Mar, Calif. The drawing shows the layout of the transect lines and the position of each fixed quadrat.

depths between 14 and 20 m in the most seaward *Macrocystis* stand directly off 8th Street in Del Mar. These continuing studies were begun in June 1967.

Within the perimeter of the study area the substratum is composed primarily of sedimentary mudstones and siltstones, coarse sand, and silt. The sea floor is somewhat flat in appearance, although low (<1.5 m) consolidated mounds and shallow ledges break up the overall visual uniformity of the bottom.

The monthly mean surface water temperatures recorded off the pier at Scripps Institution of Oceanography, approximately 24 km south of the study site, varied from a minimum of 10.1°C to a maximum of 24.6°C between June 1967 and December 1971 (Scripps Institution of Oceanography, 1968-1971). The annual mean temperature during this same period was 16.3°C. Since the water column in this area is thermally stratified, it is essential to consider bottom temperatures as well. To this end, 70 bottom temperatures were recorded at a depth of 17 m in which the mean temperature was 13.0°C with the minimum recorded temperature being 10.5°C, and the maximum being 16.0°C.

A great deal of water movement is typical to this environment (Inman and Brush, 1973) and water transparency or underwater visibility is greatly affected by the resulting sediment disturbance. Over the 5.7-yr study, the underwater visibility ranged from 0 to 20 m, the average visibility being about 3 to 4 m. However, on many dives the underwater visibility was so reduced that it was impossible to see along the bottom in the vicinity of the kelp bed.

METHODS

The study was initiated in June 1967 after several months of exploratory observations. All of the in situ observations were made while scuba diving and more than 300 h were spent underwater in this location. Most observations were made during daylight hours, however about 5 h were spent in this location between 2000 and 2200 h. The observations reported in this paper span more than 5 yr, from June 1967 through February 1973.

Initially a 100-m transect consisting of 20 brass stakes (75 cm in height) was placed along the sea floor in June 1967. One stake was placed every 5 m, and the entire array was perpendicular to the shoreline. During July 1967 the position of each attached *Macrocystis* plant growing within 1 m on either side of the 100-m transect was recorded. The condition (i.e., number of living stipes, appearance of the holdfast, etc.) of each plant was noted at various times from the beginning of the study until the plant disappeared. Also, juvenile *Macrocystis* were recorded as they appeared along the 2 m × 100 m strip.

In the fall of 1967, the main transect was extended 50 m shoreward, and during March 1968 three additional lines running parallel to the coastline were added (Figure 1). Sectioned 25-m polypropylene lines (0.60 cm in diameter) were staked into the bottom alongside of the brass stakes. The lines were sectioned so that fouling or detachment of any part would not necessitate replacement of the entire transect. All lines were marked at meter intervals with tape, and the brass stakes were numbered with line and plastic

tags. This marking system made it possible to sample any point on the transect and return to the same position even during days of marginal underwater visibility.

The entire transect area was stratified into six 2×50 m areas. Two sample points were randomly selected per stratum; at each of these 12 locations a 4-m² quadrat was placed in September 1968. Each quadrat consisted of polypropylene line, arranged in a square 2 m on a side, and held in place at each corner with galvanized spikes. Two additional 4-m² quadrats (no. 13 and 14) were added in August 1969, but in this case the locations were selected by the presence of juvenile *Macrocystis* in this part of the kelp bed. The latter two quadrats were not included in the evaluation of density or aggregation.

During September 1968 a drawing or map of each fixed quadrat was made underwater on a sheet of plastic recording natural history information and the position of each individual macroorganism. A brass meter square quadrat divided into 0.25-m² sections was used while mapping the quadrats in order to reduce the visual area being examined. Quadrats were examined at irregular intervals (i.e. monthly, bimonthly, or quarterly) by the same observer.

Data regarding density, frequency of occurrence, and distribution patterns were calculated from observations in the 12 4-m² fixed quadrats and from 48 1-m² quadrats placed at randomly chosen points along the transects. All quadrat analyses are from observations taken in August 1972. The distribution patterns of the conspicuous species were analyzed with the index of dispersion, variance/mean $\times$ (number of observations -1), described by Greig-Smith (1964). If the variance to mean ratio is significantly less than 1.0, the distribution is considered even, while an index significantly greater than 1.0 indicates an aggregated pattern of distribution. Significance is tested in a Chi square table with $n - 1$ degrees of freedom. Lack of significance indicates a random distribution. Since the results of most such indices depend upon quadrat size, we compared independently the 4-m² quadrats and the 1-m² quadrats. The only differences in the two analyses of pattern were minor and involved slight loss of significance in three of the 4-m² quadrat analyses; in each case this was a result of small numbers of individuals in the 12 larger samples. The results of the pattern analysis are given in Table 5 and are based on the 48 1-m² quadrats.

THE ALGAL ASSOCIATION

The floristic components of southern California kelp beds have been described by Limbaugh (1955); Dawson, Neushul, and Wildman (1960); North (1971); and Neushul (1971). Many of the mainland and insular kelp stands that we have surveyed in southern California appeared dissimilar with respect to the algal species present or their relative abundances. Therefore a generalized list of the algae known to inhabit these kelp communities is inadequate when describing a particular stand or comparing two or more kelp stands (Dawson, Neushul, and Wildman, 1960). The one characteristic of all mainland southern California beds appear to share is the overall domination of *Macrocystis*, in terms of both biomass (McFarland and Prescott, 1959) and apparent competition for the available light. The kelp bed at Del Mar is two layered, with the floating portion of *Macrocystis* suspended over an algal turf composed primarily of encrusting corallines. There is also a thinly scattered undergrowth of *Pterygophora californica, Laminaria farlowi*, and *Rhodymenia pacifica*. These species are taller than the corallines, but they occur so sparsely in this area that they cannot be considered a separate canopy. The algal association at Del Mar consisted of only a few species of attached macroalgae (Table 1); most of these plants were found along the margins of the *Macrocystis* bed.

TABLE 1.—The attached macroalgae found in the Del Mar kelp bed.

Bossiella orbigniana (Decaisne) Silva
Corallina officinalis var. *chilensis* (Harvey) Kutzing
Cystoseira osmundacea (Turner) C. Agardh
Desmarestia munda Setchell and Gardner
Desmarestia tabacoides Okamura
Laminaria farlowii Setchell
Lithophyllum sp.
Lithothamnium sp.
Macrocystis pyrifera (Linnaeus) C. Agardh
Pterygophora californica Ruprecht
Rhodymenia arborescens Dawson
Rhodymenia pacifica Kylin
Tiffaniella snyderae Farlow

OBSERVATIONS ON *MACROCYSTIS PYRIFERA*

The giant kelp was the most abundant and conspicuous species of brown algae within the study area. It is perennial and usually grows attached to solid substratum anchored into place

by the holdfast. In July 1967, 35 attached *Macrocystis* plants which contributed fronds to the surface canopy were recorded along the 2 × 100 m transect band (Figure 2). For convenience we have arbitrarily lumped all plants with fronds (stipe and blade) reaching the sea surface into a category as canopy adults. With the passage of time, the number of adult *Macrocystis* growing within this 100-m transect band was gradually reduced from 35 plants to a single survivor in June 1970. In addition to the plants along this part of the transect we followed 14 adult *Macrocystis* that grew along the 50-m shoreward extension of the transect (Figure 3). This shallower portion of the kelp bed displayed a similar reduction in the number of adult *Macrocystis*. In April 1968, 14 plants were recorded along this 2 × 50 m belt, however by April 1970 the last survivor had disappeared.

The dramatic fluctuations in the number of adult *Macrocystis* within this kelp stand can be detected from both in situ counts and kelp harvesting records over the past 32 yr (Figure 4). North (1971) stated "that beds five and six, lying between Del Mar and Oceanside, California have often fluctuated in this manner. These beds actually consist of approximately eight major kelp areas along about 15 km of coastline. They flourish and disappear more or less in unison, typically but not invariably with a four year period."

The general pattern for the Del Mar *Macrocystis* population seemed to be gradual attrition of the adult plants with little or no replacement over a 3-yr period, followed by recruitment after most of the adult plants had disappeared. With the addition of 40 young adult *Macrocystis* along the 100-m transect (Figure 2) during the summer of 1971 the study area again supported a density of kelp plants similar to July 1967.

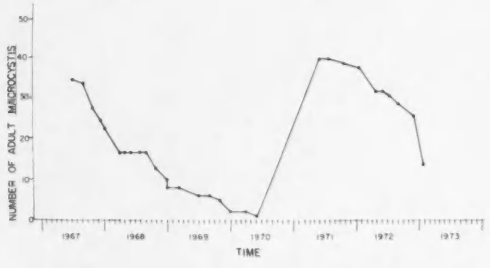

FIGURE 2.—Occurrence of adult *Macrocystis pyrifera* in the 2 m × 100 m transect (0-100 m).

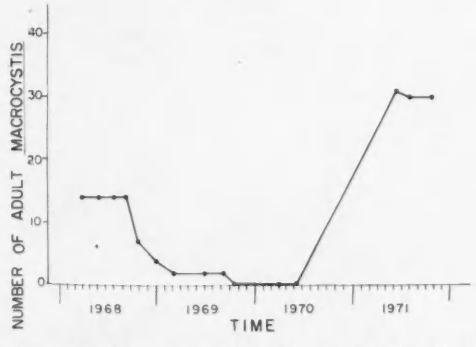

FIGURE 3.—Occurrence of adult *Macrocystis pyrifera* in the 2 m × 50 m transect (100-150 m).

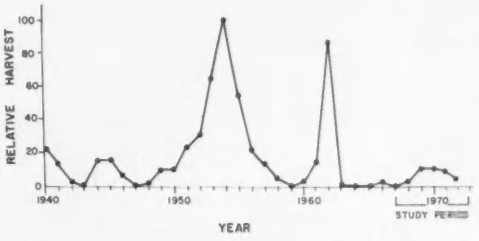

FIGURE 4.—Relative kelp harvest from bed number 5 (Del Mar). After North (1971) and Kelco Company.

Causes of Plant Mortality

Severe grazing of *Macrocystis* by sea urchins, as described by Leighton (1971) off southern California, has not been observed within this kelp stand. The two conspicuous sea urchins in this area, *Strongylocentrotus franciscanus* and *S. purpuratus* were usually observed on consolidated sedimentary mounds, under rocks, or within ledges. During both daylight and nocturnal hours the sea urchins remained in these locations, and in most instances their feeding was restricted to detritus and detached pieces of drift algae. However, *S. purpuratus* was occasionally noted within the deteriorating holdfasts of aging *Macrocystis*. In general, it appeared that there was enough drift algae for the sea urchin population to make foraging unnecessary, and we gathered no evidence that the urchins were exerting much grazing pressure on *Macrocystis*.

Fish damage to *Macrocystis* was minimal in mature plants. Most of the grazing by fishes was directed towards juvenile plants. Quast (1968b, 1971) investigated the stomach contents of fishes collected at Del Mar and found *Macrocystis* fragments in the stomachs of the labrid *Oxyjulis californica*, the kyphosid *Medialuna californiensis* and the embiotocid *Phanerodon furcatus*. He also found macroalgae as a predominant item in terms of frequency and volume in the stomachs of *Girella nigricans*. During daylight hours in this area *O. californica, Embiotoca jacksoni*, and *G. nigricans* were observed biting off portions of adult and/or juvenile *Macrocystis*. Some of the fish grazing may have been directed at the invertebrates associated with the algae, but for whatever reason, the plants were damaged by these feeding activities.

Most adult *Macrocystis* attrition recorded over the 5.7 yr was caused by detachment of the holdfast and thereby elimination of the entire plant. Plants with weakened or decaying holdfasts were particularly vulnerable to physical stress. Three factors probably accounted for most of the plant mortality in this location: 1) storms and strong surge, 2) entanglement of drifting plants with attached *Macrocystis*, and 3) kelp harvesting. Many of the kelp stands in San Diego County have been greatly thinned or almost torn away by the effects of storms (Brandt, 1923; ZoBell, 1971). Brandt (1923) reported that the La Jolla and Pt. Loma kelp beds were reduced nearly 40% in area by storms in the late winter and early spring of 1915. When *Macrocystis* plants become detached they drift along in the water column, often becoming entangled with other kelps (Figure 5). Drifting or dislodged plants thus present a potential source of mortality for attached *Macrocystis*. The stipes, blades, and holdfasts of entangled plants become so entwined that separation becomes almost impossible. We have observed as many as 18 adult *Macrocystis* entwined in one cluster near the transect. In almost every case the entanglement resulted in the mortality of the attached plant. This is a partial explanation why *Macrocystis*

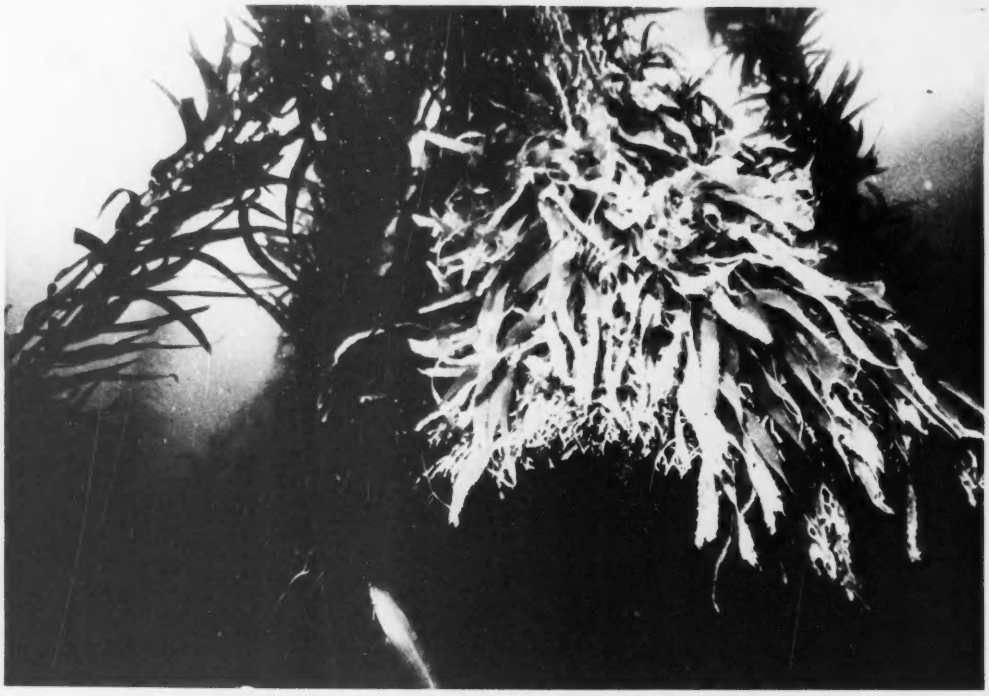

FIGURE 5.—A detached *Macrocystis* drifting through the kelp bed.

growing along the transect were frequently removed in clumps of two or three plants at a time (Table 2).

The effect of harvesting on individual plants is still inconclusive. ZoBell (1971) concluded from observations of drift seaweeds on San Diego beaches that there is no consistent relationship between kelp harvesting operations and the amount of seaweed on beaches. However, at Del Mar we found adult *Macrocystis* pulled free of the substratum following harvesting. On 6 January 1969, 10 marked plants were growing along the 100-m transect (Figure 2) and 4 plants remained in the 50-m extension (Figure 3). The seas were calm and there were no loose or drifting *Macrocystis* observed along the entire transect. The kelp bed was harvested on 7-8 January 1969. Returning to the study area on 9 January 1969 we found unattached *Macrocystis* which were either drifting in the water column or entangled with other attached *Macrocystis*. Two of the marked plants on the 100-m transect were detached from the substratum, and one plant from the 50-m extension was missing. Also, one adult *Macrocystis* from fixed quadrat number 1 was removed. These detached plants probably caused additional mortalities by entangling with other plants in the kelp bed. In summary, strong water movement, plant entanglement, and harvesting probably act in a synergistic manner on attached *Macrocystis*.

Germination, Recruitment, and Survivorship

Macrocystis undergoes a life cycle that alternates between an asexual macroscopic stage termed the sporophyte, and a sexual microscopic gametophyte stage (Brandt, 1923; Neushul and Haxo, 1963). Because of the difficulties inherent in microscopic investigation underwater we recorded recruitment only when the young sporophytes became visible. Although *Macrocystis* spores and gametophytes were probably present at different times of the year (Neushul, 1959; North, 1964), we were primarily concerned with the plants when they visually became part of the epibenthic community. A few young plants (<1 m in height) were observed in the study area during the early summer of 1967, however by the fall of that same year all of these juvenile sporophytes had disappeared. For the next 23 mo, no *Macrocystis* recruits were observed in the vicinity of the transect. During this time the overlying canopy was expanding to a point when, in December 1968, it covered approximately 90% of the 150-m transect line. Thus, insufficient light penetration resulting from shading by adult plants and water turbidity may have been key reasons for the absence of juvenile *Macrocystis* during 1967 and 1968. However, the bed was harvested in January 1969, which apparently reduced the surface canopy to about 15% cover

TABLE 2.—Stipe counts of individually tagged plants through study period. Plant number 1 survived with 7-8 stipes until August 1972. "G" means that the plant was completely gone and "O" signifies that there were no stipes but that the holdfast was still attached. Note the tendency for groups of plants to disappear together; in each case this resulted from mutual entanglement.

	Plant number																											
Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
July 1967	18	34	20	30	22	36	18	16	53	9	34	20	30	54	28	11	55	97	90	—	30	—	71	25	30	41	74	—	58	22
Sept. 1967	21	38	20	12	22	44	13	2	54	7	27	15	40	60	30	14	67	108	98	53	37	34	64	27	58	40	93	80	53	24
Dec. 1967	22	34	26	G	O	43	13	O	57	O	22	6	30	56	32	6	67	96	86	62	42	41	58	22	52	39	80	81	68	O
Jan. 1968	28	38	O			64	17		64		23	6	37	72	35	6	75	88	106	O	48	45	63	23	52	34	71	72	68	
Apr. 1968	32	31					16		60		27	G	32	G	30	4	67	63	102		46	44	G	22	42	35	74	60	G	
May 1968	34	28					10		63		28		35		31	G	73	82	115		42	53		22	52	34	78	62		
June 1968	29	22					10		49		25		36		35		81	84	123		42	52		22	46	31	75	57		
Aug. 1968	25	17					11		58		30		34		34		70	64	116		43	40		22	44	37	77	54		
Sept. 1968	30	14					9		47		30		32		38		80	70	114		42	39		24	50	36	87	64		
Nov. 1968	29	11					G		G		29		23		42		93	27	114		43	43		26	G	G	92	62		
Jan. 1969	23	12									24		22		40		—	G	127		43	40		24			G	65		
Mar. 1969	27	6									14		15		24		65		108		50	G		G				G		
July 1969	23	G									17		22		G		77		130		51									
Sept. 1969	22										14		27				66		126		54									
Oct. 1969	21										13		30				G		90		50									
Jan. 1970	25										G		23						G		G									
Apr. 1970	20												34																	
June 1970	12												G																	

along the 150-m transect. In addition to the harvesting effect, the kelp bed was aging and the canopy was being reduced through the natural attrition of older plants. More areas of the bed were gradually opened to receive increased light penetration.

The first visible germination of *Macrocystis* sporophytes occurred during August-September 1969, when plants approximately 1 to 3 cm in height appeared on or near the survey lines. Although juvenile plants were found in scattered locations throughout the kelp bed, the most dense concentrations appeared around the shoreward (eastern) end of the transect, from about 100 m to 150 m (Figure 1). Only two adult plants remained within this 2 × 50 m band transect during the summer of 1969 (Figure 3); therefore, shading of the underlying sea floor was probably minimal. Also, this shoreward edge of the bed is approximately 5 m shallower than the seaward portion and there may have been more ambient light in this part of the kelp bed. Juvenile sporophyte density ranged from 0 to 32 plants/m^2 within the fixed quadrats. *Macrocystis* recruitment was especially pronounced in the 100- to 150-m area on the transect. For this reason two additional 4-m^2 quadrats (no. 13 and 14) were added in this location when the first sporophytes appeared in August 1969. In September 1969, a total of 387 single-bladed *Macrocystis* were counted within the fixed quadrats (Figure 6). After the first month only 156 plants survived, and by June 1970 the young sporophyte population was reduced to only 5 survivors.

Most of the juvenile plant mortality was believed to be caused by plant entanglement, fish grazing, physical scouring, and/or actual burial of the plants by moving sand. Many of the young sporophytes were damaged, primarily in the region of the apical tip. These plants were inspected for invertebrate grazers, but none were found. It seems likely that the grazers were positioned in the water column because most of the grazing was located around the terminal ends of each blade. On two occasions the labrid *Oxyjulis californica* and the embiotocid *Embiotoca jacksoni* were seen nibbling on juvenile *Macrocystis*. However, because of marginal underwater visibility in this area, it was generally not possible to observe the grazing activities of fishes directly.

Physical scouring and burial is another cause of juvenile plant mortality. For example, one group of young plants (n = 36) growing within a shallow depression along the sea floor became completely covered with sand during the late fall of 1969 and never reappeared. The stipes of *Macrocystis* are quite sensitive to being enclosed or covered (North, 1971), and apparently the young plants can not tolerate burial for any length of time. In kelp beds such as Del Mar, the juvenile *Macrocystis* appear to be highly vulnerable to this physical phenomenon.

The five surviving *Macrocystis* plants that grew within the fixed quadrats continued to mature and eventually the stipes reached the sea surface. One plant perished in September 1972; however, the other four were still present within the quadrats in December 1972, 3 yr and 3 mo after germination.

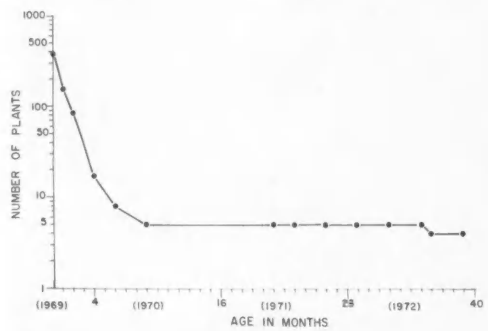

FIGURE 6.—Survivorship curve of individual *Macrocystis* which were observed to recruit in September 1969.

Plant Longevity

At the present time there is little information available in the literature on the life span of *Macrocystis* because most of the data have been collected on the longevity of individual fronds. The maximum life span of a *Macrocystis* frond was found to be about 6 mo (Brandt, 1923; Cribb, 1954; North, 1961). North (1968) reported that 3 yr were required to totally eliminate tagged mature plants within a stand of kelp off La Jolla, Calif. Most of the plants were very large at the beginning of the study, "so they probably were at least 5 years of age when they vanished, or quite likely older." (North, 1968:224).

Of the 49 adult *Macrocystis* plants originally marked along the Del Mar transect no survivors

persisted in August 1972. The oldest surviving plant lived until July 1972, an elapsed time of 5 yr. During July 1967 this plant (number 1) had 18 living stipes (Table 2). The number of stipes growing from this plant reached a maximum of 34 during May 1968; thereafter, the number of stipes slowly decreased. Based on data derived from the fixed quadrats, a *Macrocystis* plant growing in this bed with 18 stipes is at least 2 yr old. Therefore, by July 1972 plant number 1 was probably at least 7 yr of age. In addition, three other tagged plants were believed to be more than 5 yr of age at the time of their dislodgement, and four of the *Macrocystis* that grew up within the fixed quadrats were still alive after 3 yr and 3 mo (Figure 6).

Counting the number of living stipes on selected *Macrocystis* plants does not necessarily indicate the age of a kelp bed or ages of plants within the bed. For example, the number of stipes found on individual plants at Del Mar usually fluctuated with the season and the condition of the plant (Table 2). Most of the adult *Macrocystis* displayed a period during which each plant maintained a maximum number of stipes, followed by a gradual decline in the total number of stipes. At some point in the life of a Del Mar *Macrocystis* the plant no longer appears to be able to actively support a peak number of stipes.

TABLE 3.—A list of fishes observed in the kelp bed by Quast (1968a) and during this study. ++ signifies those species seen in both studies; — signifies those species seen in our study, but not reported by Quast (1968a).

Anisotremus davidsoni (Steindachner)	—
Atherinops affinis (Ayers)	++
Brachyistius frenatus Gill	++
Chromis punctipinnis (Cooper)	++
Coryphopterus nicholsi (Bean)	—
Embiotoca jacksoni Agassiz	++
Engraulis mordax Girard	++
Girella nigricans (Ayres)	++
Gymnothorax mordax (Ayres)	—
Halichoeres semicinctus (Ayres)	—
Heterostichus rostratus Girard	++
Hyperprosopon argenteum Gibbons	++
Hypsurus caryi (Agassiz)	++
Leiocottus hirundo Girard	++
Medialuna californiensis (Steindachner)	++
Oxyjulis californica Günther	++
Oxylebius pictus Gill	—
Paralabrax clathratus (Girard)	++
Paralabrax maculatofasciatus (Steindachner)	—
Paralabrax nebulifer (Girard)	—
Paralichthys californicus (Ayres)	—
Phanerodon furcatus Girard	++
Pimelometopon pulchrum (Ayres)	++
Pleuronichthys coenosus Girard	++
Pneumatophorus diego (Ayres)	—
Rhacochilus toxotes Agassiz	++
Rhacochilus vacca (Girard)	++
Scorpaena guttata Girard	++
Scorpaenichthys marmoratus (Ayres)	—
Sebastes atrovirens (Jordan and Gilbert)	++
Sebastes auriculatus Girard	—
Sebastes chrysomelas (Jordan and Gilbert)	—
Sebastes rastrelliger (Jordan and Gilbert)	++
Sebastes serriceps (Jordan and Gilbert)	—
Seriola dorsalis (Gill)	—
Sphyraena argentea Girard	—
Torpedo californica (Ayres)	—
Urolophus halleri (Cooper)	—

FAUNAL ASSOCIATION

Components of the Epifauna

Within the study area 38 species of fishes were sighted (Table 3), and 98 species of epibenthic invertebrates have been identified (Table 4). Many of the macroinvertebrates listed in the table were rarely observed, but 39 were seen on over half of the dives. A number of these species were numerically uncommon in this area, while other animals were infrequently seen because of differences in activity periods. For example, the gastropod *Cypraea spadicea* was rarely observed in exposed positions during daylight hours, but was one of the most abundant mollusks during the three nocturnal surveys made in this location. Of the 38 species of fish which we recorded, 20 species were collected in 1958 by Quast (1968a).

Epibenthic Invertebrates

Invertebrates considered in this study consisted of those species living along the sea floor that could be counted without disturbing the underlying substratum. Visually and numerically conspicuous macroinvertebrates were selected for study after data were collected on presence of species and their relative abundance in 1967. Of the 98 invertebrate species seen, only 14 species appeared to comprise the "characteristic" assemblage of epibenthic invertebrates in this kelp bed (Table 5). Characteristic epifauna were those "species that were always seen and that dominated the habitat, both numerically and in terms of their demand and impact on it." (Fager, 1968). Table 5 lists the frequency of occurrence, numerical density, pattern of distribution, and habit of each of the 14 species. Because of the importance of natural history information to an eventual synthesis of the organization of the kelp community, the following observations are presented for the 14 species. The species are discussed in order of their relative abundance.

The most abundant and frequently encountered epifaunal invertebrate in the study site during

TABLE 4.—Epifaunal invertebrates collected within the perimeter of the study area.

Porifera
- *Leucilla* (= *Rhabdodermilla*) *nuttingii* Urban
- *Leucosolenia* sp.
- *Tethya aurantia* (Pallas)
- *Verongia thiona* de Laubenfels
- *Cliona celata* Grant

Cnidaria
- *Aglaophenia* spp.
- *Corynactis californica* Carlgren
- *Epiactis prolifera* Verrill
- *Pachycerianthus* sp.
- *Tubularia* sp.
- *Balanophyllia elegans* Verrill
- *Paracyathus stearnsi* Verrill
- *Lophogorgia chilensis* (Verrill)
- *Muricea californica* (Aurivillius)
- *Muricea fruticosa* (Verrill)
- *Tealia coriacea* (Cuvier)
- *Harenactis attenuata* Torrey
- *Parazoanthus lucificum* Cutress and Peguegnat
- *Sertularia* sp.
- *Plumularia* sp.
- *Anthopleura elegantissima* (Brandt)

Annelida
- *Diopatra ornata* Moore
- *Salmacina tribanchiata* (Moore)
- *Phyllochaetopterus prolifica* Potts
- *Eudistylia polymorpha* Johnson
- *Dexiospira spirillum* (Linnaeus)
- *Spirobranchus spinosus* Moore

Arthropoda
- *Paguristes ulreyi* Schmitt
- *Loxorhynchus grandis* Stimpson
- *Taliepus nuttallii* Randall
- *Synalpheus* spp.
- *Alpheus dentipes* Guerin
- *Panulirus interruptus* (Randall)
- *Betaeus harfordi* (Kingsley)
- *Cancer anthonyi* Rathbun

Arthropoda—*Continued*
- *Hippolysmata californica* Stimpson
- *Parapleustes oculatus* Barnard
- *Balanus tintinnabulum* Pilsbry
- *Balanus pacificus* Pilsbry
- *Pachycheles rudis* Stimpson
- *Idothea resecata* (Stimpson)
- *Acanthomysis sculpta* (Tattersall)
- *Lophopanopeus frontalis* (Rathbun)
- *Ampithoe humeralis* Stimpson

Mollusca
- *Kelletia kelletii* (Forbes)
- *Mitra idae* Melville
- *Bursa californica* (Hinds)
- *Conus californicus* Hinds
- *Norrisia norrisi* (Sowerby)
- *Astraea undosa* (Wood)
- *Trivia californiana* (Gray)
- *Megathura crenulata* Sowerby
- *Cypraea spadicea* Swainson
- *Haliotis rufescens* Swainson
- *Haliotis corrugata* Wood
- *Shaskyus* (= *Jaton*) *festivus* Hinds
- *Simnia vidleri* Sowerby
- *Maxwellia gemma* (Sowerby)
- *Crassispira semiinflata* (Grant and Gale)
- *Acteon punctocaelatus* (Carpenter)
- *Mitrella carinata* (Hinds)
- *Crepidula adunca* Sowerby
- *Anisodoris nobilis* (MacFarland)
- *Glossodoris californiensis* (Bergh)
- *Dendrodoris fulva* (MacFarland)
- *Cadlina flavomaculata* MacFarland
- *Flabellinopsis iodinea* (Cooper)
- *Hinnites multirugosus* (Gale)
- *Platyodon cancellatus* (Conrad)
- *Parapholas californica* (Conrad)
- *Adula* (= *Botula*) *falcata* (Gould)
- *Lithophaga plumula* (Hanley)

Mollusca—*Continued*
- *Leptopecten latiauratus (Conrad)*
- *Lima hemphilli* Hertlein and Strong
- *Saxidomus nuttalli* Conrad
- *Octopus bimaculatus* Verrill
- *Penitella penita* (Conrad)
- *Chaeceia ovoidea* (Gould)

Bryozoa
- *Diaperoecia californica* (d'Orbigny)
- *Membranipora membranacea* (Linnaeus)
- *Membranipora serrilamella* Osburn
- *Bugula neritina* (Linnaeus)
- *Antropora tincta* Osborn
- *Thalamoporella californica* (Levinson)

Echinodermata
- *Dermasterias imbricata* (Grube)
- *Astropecten armatus* Gray
- *Astrometis sertulifera* (Xantus)
- *Henricia leviuscula* (Stimpson)
- *Patiria miniata* (Brandt)
- *Pisaster brevispinus* (Stimpson)
- *Pisaster giganteus* (Stimpson)
- *Ophioplocus esmarki* Lyman
- *Ophiothrix spiculata* Le Conte
- *Parastichopus parvimensis* (Clark)
- *Eupentacta quinquesemita* (Selenka)
- *Amphipholis* sp.
- *Ophioderma panamensis* Lutken
- *Ophiopteris papillosa* (Lyman)
- *Strongylocentrotus franciscanus* (A. Agassiz)
- *Strongylocentrotus purpuratus* (Stimpson)

Chordata
- *Styela montereyensis* (Dall)
- *Polyclinum planum* (Ritter and Forsyth)
- *Pyura haustor* (Stimpson)
- *Eudistoma diaphanes* Ritter and Forsyth

TABLE 5.—The conspicuous macroinvertebrates in the Del Mar kelp bed.

Species	Habit	Frequency[1]	Density[2]	Distribution pattern	Probability[4]
Diopatra ornata	Sessile	87/96	12.95	Aggregated	$P<0.001$
Styela montereyensis	Sessile	79/96	3.40	Aggregated	$P<0.001$
Muricea californica	Sessile	67/96	2.53	Aggregated	$P<0.001$
Kelletia kelletii	Motile	35/96	0.62	Aggregated	$0.001<P<0.01$
Parapholas californica	Sessile	22/96	0.47	Aggregated	$P<0.001$
Paguristes ulreyi	Motile	9/96	0.39	Aggregated	$P<0.001$
Muricea fruticosa	Sessile	18/96	0.27	Aggregated	$0.05>P>0.02$
Strongylocentrotus franciscanus	Motile	2/96	0.16	Aggregated	$P<0.001$
Tealia coriacea	Sessile	11/96	0.16	Aggregated	$0.001<P<0.01$
Tethya aurantia	Sessile	10/96	0.14	Random[3]	$0.05<P<0.10$
Astrometis sertulifera	Motile	12/96	0.13	Aggregated	$0.05>P>0.025$
Lophogorgia chilensis	Sessile	4/96	0.04	Random[3]	$0.70>P>0.50$
Strongylocentrotus purpuratus	Motile	2/96	0.03	Aggregated	$0.001<P<.01$
Pisaster giganteus	Motile	3/96	0.01	Random[3]	$0.30<P<0.50$

[1] Occurrence in 96 1-m² quadrats.
[2] Per m².
[3] n is small — index of dispersion inadequate.
[4] Probability of a random distribution.

August 1972 was the tubicolous polychaete *Diopatra ornata* (Table 5). *Diopatra* was seen along the transect during the early years of the study (1967-68) however, it was not until the summer of 1971 that the species was considered to be common. During August 1972, *Diopatra* occurred in all 12 of the fixed quadrats, and quadrat number 7, which contained only a few individuals in 1968, had many clumps of *Diopatra* tubes. The tubes covered an estimated 25-30% of the total area (4 m²) in the quadrat. Unpublished work of Ray Emerson (pers. commun.)[4] demonstrates that approximately 90%

[4]Emerson, R. In preparation. Reproductive biology and population dynamics of the polychaete *Diopatra ornata*. Ph.D. thesis, Univ. of Southern Calif.

of *Diopatra* tubes represent living worms. Emerson considers *Diopatra* a selective but omnivorous deposit feeder. We have seen fragments of *Macrocystis* attached to its tube apparently serving a dual function of camouflage and food reserve. The gastropod *Kelletia kelletii* and the sea star *Pisaster giganteus* were the only invertebrates seen eating *Diopatra* in this area. *Kelletia* was frequently observed penetrating either the sides or opening of the *Diopatra* tube with an extensible proboscis, and *Pisaster* was found with its stomach everted into the opening of the tube.

The solitary ascidian *Styela montereyensis* usually grows attached to rocks, shells, and *Macrocystis* holdfasts. *Styela* was found to live approximately 12 to 20 mo; however, one individual lived for more than 30 mo. Usually there is a heavy recruitment in the late summer and heavy mortality late the next spring (Figure 7). The fall *Styela* population remained reasonably constant over 4 yr (1968-72), despite the fluctuations in the population during a calendar year. A major cause of mortality in the fixed quadrats was sediment movement and strong water motion that either buried or detached the ascidians from the substratum. Three predators of *Styela* were observed: *Pisaster giganteus* and *Kelletia kelletii* frequently were seen feeding on *Styela*. On five occasions these two species were encountered feeding simultaneously on the same *Styela* (Rosenthal, 1971). In addition, we found the sea star *Astrometis sertulifera* eating *Styela* in this location.

The gorgonian *Muricea californica* was the most visually conspicuous and the third most abundant (2.53/m²) macroinvertebrate in the assemblage (Table 5). It is a colonial animal usually found growing erect from solid substratum. *Muricea californica* recruits become visible to the unaided eye when the colony is approximately 1 cm high; at this stage they appear to be at least several months old (Grigg, 1970). A decline in the *M. californica* population was recorded during the time period of this study. A total of 192 individual colonies were living within the 48-m² area in September 1968, but by December 1972 the population had declined to 119 colonies. During this time interval there were 147 mortalities and 74 recruitments recorded in the fixed quadrats (Figure 8). Grigg (1970) found a similar decrease in the *M. californica* population off Del Mar in which he recorded a relatively heavy mortality with no replacement or recruitment during a 1-yr period of observation in 1968. There are several physical factors contributing to the mortality of *M. californica* in this area. Scouring, holdfast detachment, and burial by sand are important examples. Grigg (1970) felt that two-thirds of the mortality recorded at Del Mar during 1968 resulted from physical abrasion by suspended particles, and one-third from colony detachment. Occasionally, *M. californica* growing either between the holdfasts of adult *Macrocystis* or in close proximity to an established plant died when the plant became detached and drifted away. In such cases the *M. californica* were entangled and pulled from the sea floor or were

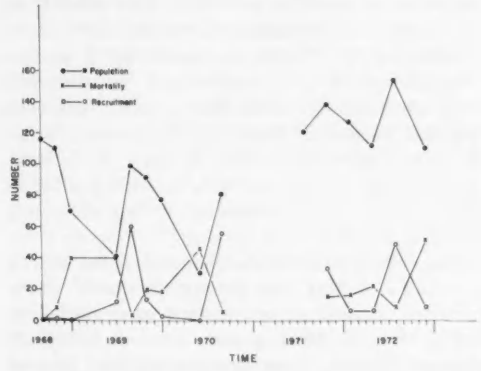

FIGURE 7.—*Styela montereyensis* in the 12 fixed quadrats (48 m²).

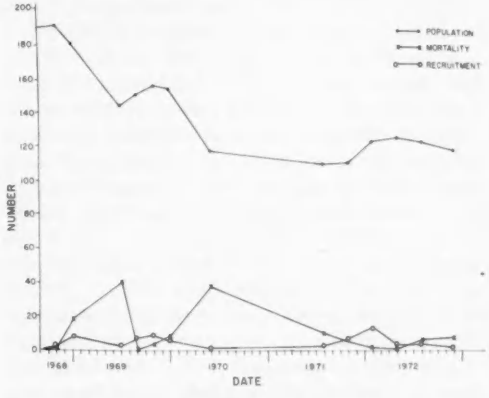

FIGURE 8.—*Muricea californica* in the 12 fixed quadrats (48 m²).

killed by increased scouring and sediment burial in the absence of the large *Macrocystis* holdfast.

The Kellet's whelk, *Kelletia kelletii*, is usually found on rocky substrata or in sand areas adjacent to more solid substratum. During August 1972 we observed a mean density of 0.62/m² in the combined samples (Table 5). On other occasions the density along the transect ranged from 0.42 to 0.75/m². Movement off Del Mar is apparently not random, for individual snails were often found in aggregated patterns of distribution. Such aggregations may reflect feeding and reproductive behavior. For example, during the height of the April-May spawning period (Rosenthal, 1970), mixed aggregations of both male and female *Kelletia* were repeatedly encountered. A few of these spawning aggregations contained between 200 and 300 individuals; however, the average spawning cluster was about 15 to 20 snails.

Kelletia is basically a carnivorous scavenger; however it does feed on live sedentary polychaetes and solitary ascidians. It has been observed eating 22 species of invertebrates and 3 species of dead or moribund fish in the subtidal waters off San Diego County (Rosenthal, 1971).

Predators of *Kelletia* include the asteroids *Pisaster giganteus*, *P. brevispinus*, and *Astrometis sertulifera*, and the cephalopod *Octopus bimaculatus* (Rosenthal, 1971). Few other predators are known, although Limbaugh (1955) reported finding juvenile *Kelletia* in the stomachs of pile perch, *Rhacochilus vacca*.

Parapholas californica, a bivalve clam, was the most conspicuous terrigenous borer off Del Mar. It primarily bores into sedimentary rocks consisting of consolidated mudstones and siltstones. Within the 12 fixed quadrats the *Parapholas* population density was 0.54/m². During the monitoring period there were two recruitments and three mortalities recorded in these quadrats. *Pisaster giganteus* and *P. brevispinus* occasionally prey upon *Parapholas* in this location, as they do in other nearshore areas off San Diego County (Rosenthal, 1971). Predation by sea stars often has the additional effect of breaking the substratum surrounding the clam.

Paguristes ulreyi is a relatively large, pubescent hermit crab. Almost all were found in discarded *Kelletia* shells; however, a few crabs were also seen in the shells of *Bursa californica*. *Paguristes* was seen throughout the study area, although its most frequent habitat appeared to be the siltstone ledges and consolidated sedimentary mounds located towards the seaward edge of the bed. Each year large aggregations (to 220/m²) of *Paguristes* were observed in this area from August through October, the crabs often being stacked several layers thick. *Paguristes* is a scavenger (Pequegnat, 1964), a conclusion supported by our observations of it feeding upon dead invertebrates and pieces of detached algae. *Octopus bimaculatus* was the only known predator of *Paguristes* in this location. On two occasions, *O. bimaculatus* was observed moving shells inhabited by *Paguristes* and one individual was encountered while feeding on a *Paguristes*.

Muricea fruticosa is similar in appearance to *M. californica*, but is usually bushier with a rusty-brown coenenchymal layer and white polyps. Both species of *Muricea* were observed growing on similar or identical substrata. The mean of 0.27 colonies/m² in this area (Table 5) is in agreement with the estimate of 0.25 colonies/m² of Grigg (1970). The *M. fruticosa* population was almost balanced with respect to mortality and recruitment. Fourteen *M. fruticosa* were recorded in the fixed quadrats during September 1968, and 13 individual colonies were found in these same quadrats during December 1972, but during this period 17 mortalities and 16 recruitments were noted. No predators of *M. fruticosa* were observed in the study area, and causes of mortality are believed to be similar to those reported for *M. californica*.

Tealia coriacea is a solitary, medium sized (4 to 7 cm) sea anemone. It attaches to solid substratum and usually the column is partially buried or enclosed by sediment. Two mortalities and three recruitments were recorded in the fixed quadrats. One *Tealia* was eaten by a leather star, *Dermasterias imbricata*, and the other died from an unknown cause. *Dermasterias* has been reported to eat *Tealia* spp. and other sea anemones in the Pacific Northwest (Mauzey, Birkeland, and Dayton, 1968), and may on occasion be an important source of mortality in California kelp beds.

The largest and most conspicuous sea urchin seen off Del Mar was *Strongylocentrotus franciscanus*. Individual test diameters ranged from 5.5 to 18.2 cm. Most of these animals inhabited the sedimentary mounds and boulders located towards the seaward edges of the kelp stand.

The trophic role displayed by *S. franciscanus* in southern California kelp communities has been adequately described (Limbaugh, 1955; Leighton, 1971; North, 1971). *Strongylocentrotus franciscanus* is important because it often overexploits its algal resources in areas of high sea urchin density. Despite the fact that this species is highly motile, foraging movements on attached kelps were not witnessed in this kelp bed. The *S. franciscanus* population appeared to be sustained by snagging detached pieces of macroalgae that drifted along the sea floor. The only predator we observed feeding upon live *S. franciscanus* in this area was the labrid *Pimelometopon pulchrum*.

Tethya aurantia, a hemispherical shaped sponge, attains a circumference of at least 25 cm and is usually found attached to rocks and consolidated sediments. There were two mortalities and three recruitments recorded in the fixed quadrats. One mortality was attributed to sediment burial, and *Dermasterias imbricata* was observed feeding on *Tethya* in the vicinity of the transect. Rosenthal and Chess (1972) reported *Dermasterias* to be a predator of *Tethya* in the sublittoral zone off Pt. Loma, Calif.

Astrometis sertulifera was the most abundant (0.13/m²) sea star encountered off Del Mar (Table 5). This estimate of abundance is probably conservative because *Astrometis* is relatively small (4 to 6 cm in radius) and individuals are somewhat cryptic in habit. The most frequent habitat of *Astrometis* off Del Mar was the undersides of rocks and the interstices of *Macrocystis* holdfasts. It appears to be ideally suited for preying upon the assemblage of organisms found associated with the holdfasts of *Macrocystis*. *Astrometis* was observed eating juvenile *Kelletia kelletii* (gastropod), *Conus californica* (gastropod), *Mitrella* sp. (gastropod), *Styela montereyensis* (ascidian) and juvenile *Strongylocentrotus purpuratus* (echinoid) in this study. Leighton (1971) mentioned that *Astrometis* feeds heavily on juvenile sea urchins off southern California. No predators of *Astrometis* were observed in the study area; however, Rosenthal and Chess (1972) found that 4% of 437 feeding *Dermasterias* were eating *Astrometis*.

The gorgonian *Lophogorgia chilensis* is one of the most exquisite macroinvertebrates in this region. It usually grows in an upright manner attached to solid substratum. A few small colonies were found growing attached to *Muricea californica*. *Lophogorgia* was not nearly as abundant as *M. californica* or *M. fruticosa*; the mean density during August 1972 was 0.04/m² (Table 5). There was one mortality and one recruitment recorded in the 48-m² quadrat area during 1968-72. No predators of *Lophogorgia* were observed in this kelp bed and causes of colony mortality are probably similar to those of *Muricea* spp.

The purple sea urchin, *Strongylocentrotus purpuratus*, ranged in size from 15 to 68 mm, with a median size of 42 mm (n = 82). In contrast to the low density in this location (0.03/m²), other kelp stands off southern California have been found to contain as many as 77 *S. purpuratus*/yd² (Leighton, 1971). The most frequent habitat of *S. purpuratus* off Del Mar was the undersides of rocks; however, individuals were also found on consolidated mounds and siltstone ledges. A few individuals were noted within the holdfasts of adult *Macrocystis*; however, we believe the incidence of holdfast infestation is low in comparison to other San Diego County kelp beds. *Strongylocentrotus purpuratus* is a herbivore well known to overexploit its algal resources (Leighton, 1971; North, 1971). In the Del Mar area most of the purple sea urchins were observed eating detritus and drift algae; rarely were the attached macroalgae grazed upon.

Dermasterias imbricata (Rosenthal and Chess, 1972), *Astrometis sertulifera* (Leighton, 1971; pers. observation), and *Pimelometopon pulchrum* (Limbaugh, 1955; pers. observation) are three known *S. purpuratus* predators which inhabited the study area.

Pisaster giganteus is one of the most abundant and widely distributed sea stars found off southern California. Although visually conspicuous at Del Mar, *Pisaster* was not nearly as abundant (0.01/m²) as it was in some of the other kelp beds (i.e. Pt. Loma, La Jolla, Catalina Island) we surveyed between 1968 and 1972. The diet of *Pisaster* has been partially quantified (Rosenthal, 1971). Although it was occasionally observed scavenging, it primarily feeds on live animals which, in this area, include *Astraea undosa* (gastropod), *Conus californicus* (gastropod), *Kelletia kelletii* (gastropod), *Botula falcata* (pelecypod), *Hinnites multirugosus* (pelecypod), *Lithophaga plumula* (pelecypod), *Parapholas californica* (pelecypod), *Pennitella penita* (pelecypod),

Diopatra ornata (polychaete), and *Styela montereyensis* (ascidian).

DISCUSSION

During the years of this study (1967-73) there was a pronounced oscillation in the number of adult *Macrocystis* in the study area. Partially concurrent with these in situ observations has been a fluctuation in the amount of kelp harvested in this area since 1940 (Figure 4). The disappearance or detachment of adult *Macrocystis* along the transect was usually related to physical stress from an increase in water motion and/or entanglement with detached, drifting kelp plants. Storms, particularly during the months of October through April, seem to be the major cause of plant mortality in this bed. For example, during a 2-mo period (December-February 1973), 46% of the adult *Macrocystis* were lost along the transect (Figure 2). There is historical evidence of severe storm mortality as Brandt (1923) reported the La Jolla and Pt. Loma kelp beds were severely diminished in area by storms in 1888-89 and 1915. Doty (1971) also reports that storms have important effects on the standing crop of algae in Hawaii.

Another cause of plant attrition was commercial harvesting. Four tagged *Macrocystis* representing 21% of the marked plants in the study area were detached from the substratum during a kelp harvesting operation in January 1969. However, this rate of mortality could be higher than the harvesting attrition rate in other beds because of the relatively unstable substratum of the north San Diego County kelp beds. Certainly a preharvest consideration should be given to the actual cutting technique best suited to each individual stand of kelp.

The vulnerability of adult *Macrocystis* to entanglement and detachment would appear to result in the development of a multiage class kelp bed in which there are patches of cohorts or plants of the same age class. That is, the drifting and entanglement is rather localized and results in distinct patches of the canopy being cleared. Thus, germination and recruitment take place not only around the periphery of the bed, but also within central portions. This spatial heterogeneity of different aged *Macrocystis* may add stability to a particular kelp bed as mature, perhaps more secure plants are growing adjacent to both young and senile plants. During February 1972, it was estimated that the Del Mar bed was composed of at least four age classes of *Macrocystis*.

The paucity of juvenile *Macrocystis* sporophytes during the first 23 mo of the study was believed to be related to the establishment of a well-developed adult canopy, turbidity of the water column, and the relatively unstable substratum. These factors are interrelated since they contribute to the absorption and scattering of the available light necessary for germination and sporophyte development. A layer of fine sediment (silt) remained along the bottom during the entire study period, and this silt was usually suspended by increased water motion. The Los Penasquitos salt marsh located approximately 2 km southeast of the study site could be a source of much silt. Whatever the source, this sediment layer seems to be a general feature of most north San Diego County kelp beds, and as it contributes to a reduction in the submarine light and physically scours the substratum, it probably has a strong negative effect on *Macrocystis* recruitment. Despite these limiting factors, young *Macrocystis* sporophytes appeared in the Del Mar bed during August 1969. The reduction of the kelp canopy from natural attrition and harvesting probably paved the way for the late summer germination and recruitment. Following recruitment of these young plants there continued to be a strong attrition as only 4 of the original 387 sporophytes growing within the fixed quadrats survived the 3.25 yr (to December 1972).

Many of the same physical parameters that influence the *Macrocystis* population at Del Mar appear to effect the distribution, frequency of occurrence, and abundance of the fauna. Quast (1968a) determined from three fish collection sites off Del Mar, Bathtub Rock (San Diego County), and Papalote Bay, Baja California that Del Mar was lowest in fish species diversity, despite the fact that it covered the greatest area. He concluded that the differences between the three areas were due to differences in the amount of shifting sediment and the durability of the rocky substratum. Furthermore, he found a positive correlation between the degree of bottom relief and the abundance and species diversity of fish.

The epibenthic invertebrates are similarily affected by the physical characteristics of the habitat. The aggregated distribution patterns of

such sessile species as *Muricea californica*, *Styela montereyensis*, and *Parapholas californica* (Table 5) probably reflect physical heterogeneity within the Del Mar study site. The aggregated distribution patterns of motile species (*Kelletia kelletii*, *Paguristes ulreyi*, and *Strongylocentrotus franciscanus*) are probably related to aspects of their foraging and/or reproductive behavior as well as to the physical heterogeneity of the habitat.

The species composition of the epifauna was reasonably constant, however, the abundances of some species has undergone change during the 5.7 yr. The most pronounced population change occurred with the tube dwelling polychaete *Diopatra ornata*. Although this species was recorded within the study area during 1967-68, it was somewhat rare and individuals were not noted within the 12 fixed quadrats until 1971. By August 1972 however, *Diopatra* was the most abundant and most frequently encountered macroinvertebrate in the Del Mar kelp bed (Table 5). Reasons for the *Diopatra* population increase are unknown at this time.

During the same time period the *Muricea californica* population decreased from 192 to 119 colonies during 4.25 yr (Figure 8), despite considerable recruitment of small identifiable colonies. In contrast to the decline in the *M. californica* population at Del Mar, Grigg (1970) studied a population of *M. californica* off La Jolla which was relatively stable with respect to mortality and recruitment. Differences between these two sea fan populations were believed to be due to the physical characteristics of each habitat (Grigg, 1970).

The *Styela montereyensis* population had a reasonably predictable seasonal oscillation, usually reaching a peak during the late summer and fall (Figure 7). The maximum annual population ranged from 81 to 153 individuals. The average life span of *S. montereyensis* is shorter (12 to 20 mo) than some of the other members of this community such as *Muricea californica*, which is thought to reach at least 50 yr of age (Grigg, 1970). Three species: *Pisaster giganteus*, *Astrometis sertulifera*, and *Kelletia kelletii* feed upon *Styela* in this area; however, natural predation is slight in proportion to the heavy mortality caused by strong water motion and sediment burial. Other Del Mar invertebrate populations were somewhat more constant. For example, the *Muricea fruticosa* population remained relatively constant over the monitoring period (changing from a total of 14 to 13), despite 17 mortalities and 16 recruitments recorded in the fixed quadrats.

There is sufficient evidence of trophic interaction to present a very qualitative food web (Figure 9). Two of the predators, *Pisaster giganteus* and *Astrometis sertulifera* feed upon living members of the community; the diet of the former species is probably better understood (Rosenthal, 1971), because it is seen more often. While both asteroid species attack a variety of prey, mollusks appear to be the major food items off Del Mar. In addition, *Dermasterias imbricata*, *Pisaster brevispinus*, *Octopus bimaculatus*, and *Pimelometopon pulchrum* have been added to this food web. We have only qualitative data on the diets of these four species. Two other carnivores, *Kelletia kelletii* and *Paguristes ulreyi*, generally feed upon moribund or decaying animal matter, but they occasionally eat live organisms (Rosenthal, 1971). The rest of the generalized food web represents lower trophic levels.

The biotic components and temporal population changes recorded off Del Mar should not be interpreted as "characteristic" of all southern California kelp beds. Although the Del Mar bed closely resembles kelp stands off northern San Diego and Orange Counties, it appears to be different from those at La Jolla and Pt. Loma.

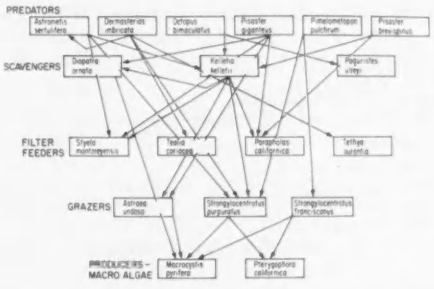

FIGURE 9.—A qualitative food web that depicts trophic interaction in the Del Mar kelp bed.

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THE SWIMMING CRABS OF THE GENUS *CALLINECTES* (DECAPODA: PORTUNIDAE)

AUSTIN B. WILLIAMS[1]

ABSTRACT

The genus *Callinectes* and its 14 species are reevaluated. Keys to identification, descriptions of species, ranges of variation for selected characters, larval distribution, and the fossil record as well as problems in identification are discussed. Confined almost exclusively to shallow coastal waters, the genus has apparently radiated both northward and southward from a center in the Atlantic Neotropical coastal region as well as into the eastern tropical Pacific through continuous connections prior to elevation of the Panamanian isthmus in the Pliocene epoch and along tropical West Africa. Eleven species occur in the Atlantic, three in the Pacific. *Callinectes marginatus* spans the eastern and western tropical Atlantic. *Callinectes sapidus*, with the broadest latitudinal distribution among all the species (Nova Scotia to Argentina), has also been introduced in Europe. All species show close similarity and great individual variation. Both migration and genetic continuity appear to be assisted by transport of larvae in currents. Distributional patterns parallel those of many organisms, especially members of the decapod crustacean genus *Penaeus* which occupy similar habitats.

The blue crab, *Callinectes sapidus* Rathbun, a staple commodity in fisheries of eastern and southern United States, is almost a commonplace object of fisheries and marine biological research, but its taxonomic status has been questionable for a long time. Other members of the genus also have questionable taxonomic status, and they are difficult to identify. In a time when expanding interest in species easily exploitable for food has generated new research, we can benefit from a fresh look at the component species of this important genus in order that major areas of study such as fisheries biology, ecology, zoogeography, embryology, and physiology can proceed on a stable nomenclatural basis. The purposes of this paper are to: 1) synonymize nomenclature, 2) characterize the species, 3) discuss variation in morphology, 4) provide illustrations and keys to identification, 5) delineate geographic distribution of species, 6) provide remarks on ecological associations, 7) contribute to resolution of the fossil record, and 8) document evidence and provide a list of identified specimens in major museums of the world.

HISTORY

Crabs of the genus *Callinectes* have an anecdotal record dating from early explorations of the Western Hemisphere. Perhaps the earliest listing among natural assets in the New World is Thomas Hariot's (1588) mention of "*Sea crabbes*, such as we have in England." A similar record is Marcgrave's account in 1648 (Lemos de Castro, 1962) of a South American *Callinectes* [= *danae* Smith (1869)], one of the common portunids used for food. D. P. de Vries in 1655 (Holthuis, 1958) referred to the eating qualities of blue crabs in the New York area and likened the white and orange color of their chelipeds [females] to colors of the House of Orange. Lawson (1714), recounting his years among the Indians in the Carolinas, may have initiated the tale of raccoons fishing for crabs in marshes with their tails, but more factually he wrote [undoubtedly of the blue crab, *C. sapidus* Rathbun (1896)], "the smaller flat Crabs I look upon to be the sweetest of all Species . . . the Breadth of a lusty Man's Hand . . . . These are inumerable, all over the salts of Carolina . . . taken not only to eat, but are the best Bait for all sorts of Fish, that live in the Salt-Water."

Holthuis (1959) thought that de Geer (1778) probably represented *Callinectes bocourti* A. Milne Edwards (1879) under the name "Crab de l'ocean" when he described a swimming crab from Surinam in general terms as *Cancer pelagicus*. Ordway (1863) considered de Geer's species synonymous with *Lupa sayi* Gibbes (1850), and Rathbun (1896:350) stated "Figures 8, 9 and 11 correctly represent neither of these species, nor are they applicable to any species of *Callinectes*, while, on the other hand, Figure 10 shows the narrow abdomen characteristic of that genus." Since *C. bocourti* is the commonest portunid in Surinam, abundant enough to be marketed, and

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certain of de Geer's figures can be interpreted as *Callinectes*, Holthuis's conclusion seems reasonable.

Bosc (1802) gave a thumbnail natural history sketch for *C. sapidus* in South Carolina comparing crudely in its accuracy with some modern accounts, but he used the name *Portunus hastatus* along with a description taken from J. C. Fabricius which applied to a European species.

Thomas Say (1817) was the first naturalist to give a description of the common blue crab of the eastern United States, calling it *Lupa hastata*, in what he intended as a redescription of *Lupa hastata* (Linn.), a species known from the Mediterranean (Rathbun, 1896).

A few years later Latreille (1825) gave the name *Portunus diacantha* to the common blue crab of eastern United States accompanied by a poor description that applied to more than one species. Say and Latreille, plus perhaps De Kay (1844) who published a description and beautifully colored plate of what he called *Lupa dicantha* [= *C. sapidus*] from New York, account for the main early treatments of *Callinectes* by naturalists.

Search of newspaper and popular journal files could yield a harvest of fact and fiction about these crabs culminating perhaps in accounts of the "crab derbies" held in recent years to promote marketing in crab producing states of the eastern seaboard of the United States. Crab stories abound and crab fishing techniques are similar in all countries where *Callinectes* occurs. It is not surprising, therefore, that this profusion has carried over into the scientific literature where scholars have bequeathed a complex nomenclature in numerous contributions.

Scholarly systematic work on the whole genus was last presented by Rathbun in 1896 as a general revision and amended in 1897. There is no need to clutter the text here by recalling the parade of specific epithets employed in the game of taxonomic musical chairs played by a succession of authors. Each built on the foundation of previous work, usually as collections substantially increased in museums, but many minor papers were reports on expeditions extending the bounds of known geographic ranges for certain species. Details of these histories may be followed in the synonymies, but the principal studies should be placed in perspective as an introduction, and in reviewing them I repeat part of Rathbun's (1896) review.

William Stimpson (1860) created the genus *Callinectes* to contain portunids in which the males have a T-shaped abdomen and the merus of the outer maxillipeds is short, sharply prominent, and curved outward at its antero-external angle. He regarded as one species "the common American *Lupa diacantha* (Latreille)" in his new genus, and doubtfully distinguished a second, *L. (= Callinectes) bellicosa*, which he had described (1859) from the Gulf of California. We now know that the second of Stimpson's generic characters is nearly valueless because other portunids have similar third maxillipeds, but the narrow sixth segment of the T-shaped abdomen of males holds and is reinforced by absence of an internal spine on the carpus of the chelipeds in *Callinectes*.

The limited view of the genus held by Stimpson was soon broadened by Ordway (1863) who recognized nine species distinguished in part by structure of the male first pleopods. Ordway restricted the name *diacanthus* to a Brazilian form described by Dana (1852) which we now know as *C. danae*. The common blue crab of the eastern United States was given Say's (1817) name *hastatus*, Stimpson's *bellicosus* retained, and six new species named. Ordway's study of crustaceans was diverted by the Civil War, and he remained in military life until his death in 1897. Poor communication may have led to Ordway's confusion in nomenclature, but his concept of species based on material then available was remarkably clear.

Latreille's (1825) *diacantha*, though valid, was never widely recognized because of its poor definition. Various *"diacanthas"* were employed for 139 yr finally ending in official suppression of Latreille's ill-starred name in 1964 for purposes of nomenclatural stability. Smith (1869) substituted *C. danae* for Dana's Brazilian *C. diacantha*.

Then followed an interval dominated by A. Milne Edwards's revision of the Portunidae (1861) and his review of the Crustacea of Mexico (1879). Milne Edwards at first did not recognize *Callinectes* as a distinct genus but later accepted it. He conservatively viewed *Callinectes* species as "varieties" of *diacanthus* (adding five new ones to Ordway's nine in 1879), and the influence of his ideas pervaded the field for a long time, leading eventually to Rathbun's revisionary papers. Milne Edwards's reasoning was not without merit for the genus is close to other portunids. Indeed, its validity as a distinct unit was again challenged for a time by Stephenson and Campbell (1959) and Stephenson (1962) during reassessment of

Indo-Pacific Portunidae, but later left intact (Stephenson, Williams, and Lance, 1968).

In 1896 Rathbun recognized the following numbers of species: western Atlantic, six species and one subspecies (Rathbun never treated the nominal subspecies as anything but a full species); eastern Pacific, four species; eastern Atlantic off Africa, one species and one subspecies. The list was almost immediately altered (1897) by name recombinations, elevation of subspecies, description of a new species, and extension of known geographic ranges. This brought the numbers to: western Atlantic, six species and one subspecies; eastern Pacific, four species; eastern Atlantic off Africa, four species. There the inventory rested until 1921 when Rathbun revised the African species, reducing them to three but noting a doubtful subspecies reported from Europe (Bouvier, 1901) greatly resembling *C. sapidus* of the United States. In 1930 Rathbun published the third of a four-volume work that serves as the standard reference on American crabs. In this she reduced the recognized species in the eastern Pacific by one. Collaterally she treated fossil members of the genus, describing three new species from the Oligocene and Miocene of Middle America (1919b), and two more species from similar ages in North America (1935). One of these from the Miocene (=?) of Virginia and Florida was considered identical with living *C. sapidus*.

By 1930 the genus seemed stabilized, but Rathbun herself had introduced confusion in 1907 by describing a juvenile *Portunus* from the South Pacific as *Callinectes alexandri*. This error bore fruit years later in helping to generate doubt concerning validity of the genus (Stephenson and Campbell, 1959). During the same year that Rathbun's cancroid treatise appeared, Contreras (1930) described two new species in a little known paper, one from the Gulf of California and another from the Gulf of Mexico. Capart (1951) and Monod (1956) both supported Rathbun's analysis of West African forms, and in shedding more light on the introduction of *C. sapidus* into European waters (first noticed in 1901) erased Rathbun's doubts about a poorly documented subspecies from that area. They also pointed out difficulties in identifying some specimens. The introduction of *C. sapidus*, documented by numerous authors, was reviewed by Holthuis (1961, 1969). Following petition of Holthuis (1962), the International Commission (1964), to avoid confusion in nomenclature of such a well-known species, made *Callinectes sapidus* Rathbun the type species of the genus and suppressed the long dormant *Portunus diacantha* Latreille, 1825. Garth and Stephenson (1966) confirmed Rathbun's interpretation of the eastern Pacific *Callinectes*, and Williams (1966) described a new species from the Carolinian Province of North America.

Such was the status of the species problem when the present study was undertaken. Numerous authors had expressed difficulty in making identifications, especially of juvenile material. Geographic limits for species seemed ill defined. Few attempts to analyze large series systematically had been attempted, but results of work in fisheries management indicated that populations within species might be distinct. Mindful of this and aware of series of specimens in museums, a review of the group seemed profitable. Simultaneously, Taissoun (1969, 1972) began study of *Callinectes* in Venezuela finding a form endemic to Lake Maracaibo. It is likely that new approaches such as ecological and larval studies may continue to elucidate variation in the genus.

CHARACTERS OF SYSTEMATIC VALUE

The gross features of morphology having greatest usefulness in distinguishing species of *Callinectes* are (Figures 1, 2): viewing dorsally, 1) the number, shape, and arrangement of frontal teeth, 2) shape of the metagastric area, 3) shape and curvature of the anterolateral teeth and the lateral spine, 4) granulation of the dorsal surface; viewing ventrally, shape of male and mature female abdomen. Shape of the chelipeds is also useful, as are the colors in fresh specimens. In addition to gross features, male first pleopods (Figures 18-21) are diagnostic, and shapes of female gonopores (Figures 22-23) are aids to identification.

Body proportions.—Proportions of the body in both sexes change with growth until a characteristically male or female form develops. The carapace of males becomes relatively broader than that of females, with lateral spines accentuated; in especially large individuals of some species the metagastric region tends to be somewhat sunken at its side and rear margins. Females have a dorsally tumid appearance, with the carapace more uniformly inflated and granulated and relatively not so broad nor with lateral spines so accentuated

as in males. Body heights are alike in the two sexes.

Spines.—All spiniform characters, poorly developed and rounded at the apices in juveniles, gradually assume conformation characteristic of the species as growth progresses.

Chelipeds.—All species in the genus have the hands of the chelipeds (Figures 3-17) modified into a major chela (crusher, usually on right side) and a minor chela (cutter, usually on left side)—heterochelic and heterodont (Schäfer, 1954; Števčić, 1971). Loss of the major chela induces a well-known reversal at the next molt with the new hand becoming a minor chela. A few individuals have two minors, but almost none exhibit two major chelae. Size and strength of the major hand vary a good deal, each species having a sometimes ill defined but characteristic shape. In all, especially among males, the dactyl of the major chela has a strongly developed proximal tooth which closes against a molariform complex on the propodus (Schäfer, 1954). A decurved lower margin near the base of the propodal finger opposite the proximal crushing apparatus on opposed edges of the fingers accompanies development of the complex, and in huge males of some species is a prominent feature. Teeth distal to the molariform complex of the major chela are more sectorial in structure, but not so sharp as those on the minor hand. Sectorial teeth of both hands tend to be arranged in triads, a large central tooth flanked by smaller ones, but there is much variation. In old individuals no longer molting or molting infrequently, the proximal crusher teeth become worn, occasionally almost obliterated. Size and wear vary with species and are undoubtedly associated with feeding habits. *Callinectes sapidus,* for example, is known to feed on the American oyster, *Crassostrea virginica,* and other mollusks. Other species of *Callinectes* probably have similar feeding habits, but these are not well documented.

Secondary sexual structures.—Immature females have a triangular abdomen (Figure 2) with most segments indistinguishably fused, but at the terminal maturation molt (Churchill, 1919) all segments become free. The abdomen of mature females has a variable but roughly characteristic shape in each species. Distal portions of the abdomen in immature males also have a developing shape which becomes characteristic of the species in adults.

Primary sexual structures.—The copulatory apparatus of male *Callinectes* has been recognized as a good separator of species since the time of Ordway (1863), but until recently no one used fine structure of these organs as serious aid to identification. Snodgrass (1936) and Cronin (1947) both described the external male sexual apparatus, and I here adopt Snodgrass's term "first gonopod" for the first male pleopod. The first gonopod is essentially a narrow flat plate rolled longitudinally into a cylinder that may be variously curved and twisted, terminating in a tip varying from nearly tubular to a simply flared trough. First gonopods of each species have characteristic shapes, but there is individual variation reinforced by age, molt stage, wear, and irregularity in preservation. The distal portion of each first gonopod is armed with retrogressive articulated spinules, exceedingly tiny and rather unevenly distributed in one set of species having short first gonopods—*C. gladiator* Benedict (1893), *marginatus* A. Milne Edwards (1861), *ornatus* Ordway (1863), and *similis* Williams (1966) (Figures 18a-d, 20a-d), as well as in a second set with relatively longer first gonopods—*C. arcuatus* Ordway (1863), *danae,* and *exasperatus* (Gerstaecker, 1856) (Figures 18e-g, 20 e-i), but larger and arranged in longitudinal bands among species with long curved first gonopods in a third set—*C. bellicosus, bocourti, latimanus* Rathbun (1897), *maracaiboensis* Taissoun (1972), *rathbunae* Contreras (1930), *sapidus,* and *toxotes* Ordway (1863) (Figures 18h-j, 19, 20j-p, 21). In the last group, the spinules are irregular in size showing evidence of breakage and replacement during growth. Moreover, first gonopods of certain species bear slender setae. In *C. arcuatus* and *danae,* with first gonopods of moderate length, the setae are subterminal (Figure 20e-h) but in others with longer first gonopods [*C. bellicosus, latimanus, maracaiboensis, rathbunae, sapidus,* and *toxotes* (Figures 20j-p, 21)] they are arranged along the shaft at levels between the fifth to seventh thoracic sternites in a single sternomesial row following the twist of the appendage. The setae are relatively largest in *bellicosus* (Figure 20j, k).

Structure of the female gonopores covered by the abdomen and located near the midline on the sixth thoracic somite (Snodgrass, 1936) is less useful as a specific character than that of the male first gonopod, but even here there are some conformational types. Each gonopore leads via a spermathecal duct (vagina) to a spermatheca

which in turn is connected to oviduct and ovary, but it is the gonopore alone that shows crude structural specificity. Hartnoll (1968) showed that the gonopore of portunids is an uncovered structure often rounded laterally and pointed mesially, whose margin is the "rigid integument of the sternum, while the lumen is normally blocked by bulges of the flexible integument which comprises the lining of the vagina." In the set of species having males with long first gonopods, the gonopores of females are paraboloid in outline (Figures 22i-l, 23a-c). Parallels with the other two sets of male gonopod types are less pronounced. Of the intermediate second set, female *C. arcuatus* and *danae* have asymmetrically ovoid gonopores (Figure 22e, f); *exasperatus* has an elongate sinuous gonopore with shelflike overgrowth on the cephalic border (Figure 22g), and *bellicosus* fits into this group (Figure 22h). Females corresponding to the set of males with short first gonopods have gonopores varying from broadly open paraboloid in *C. ornatus* (Figure 22d) to increasingly narrowed openings in *C. gladiator* and *marginatus* (Figure 22b, c), culminating in the narrow transverse slit of *C. similis* (Figure 22a).

MEASUREMENTS

The foregoing discussion shows that measurements must be taken from adults if they are to have systematic usefulness because the young are proportionally different from adults as well as being incomplete for secondary sexual characters. Some species are larger than others and certain proportions are considered useful in keys for identification (Rathbun, 1930; Garth and Stephenson, 1966). Certain populations within species may deviate from the "typical." Initially I thought that analysis of morphometric characters might help to define differences among species as well as among populations within species.

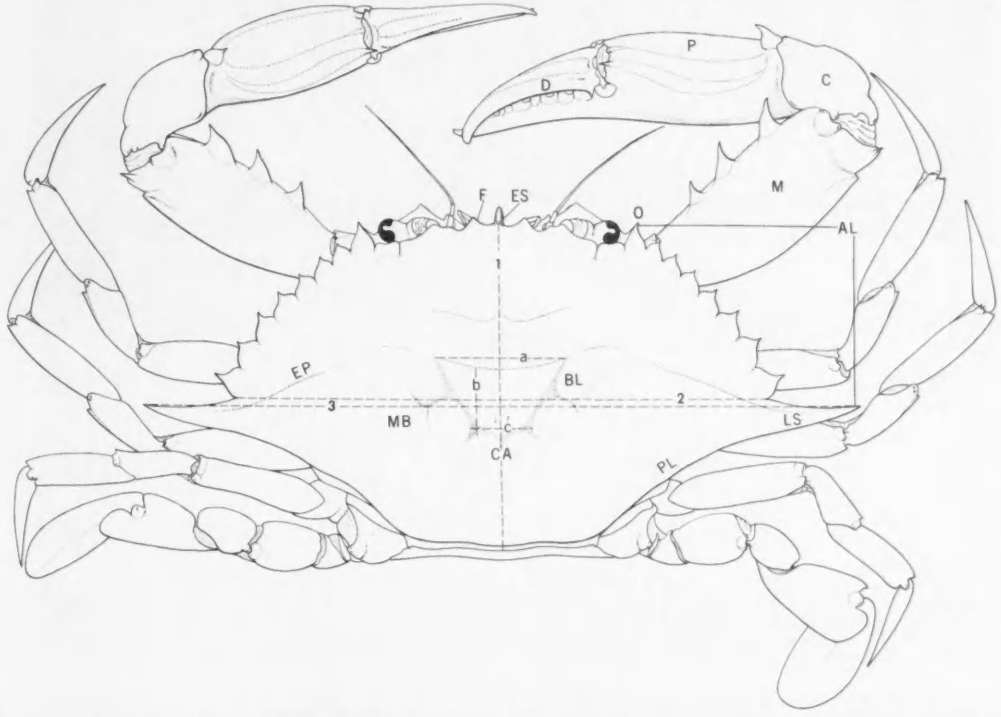


FIGURE 1.—Mature male *Callinectes sapidus* from North Carolina in dorsal view (× 1). Measured features indicated by numbered lines: 1, length; 2, width to base of lateral spines; 3, width including lateral spines; dimensions of metagastric area — a, anterior width, b, length, c, posterior width. Other features included in descriptions: (carapace) F, frontal teeth; O, outer orbital tooth; AL, anterolateral teeth; LS, lateral spine; PL, posterolateral margin; EP, epibranchial line; ES, epistomial spine; MB, mesobranchial area; CA, cardiac area; BL, branchial lobe; (cheliped) M, merus; C, carpus; P, propodus; D, dactyl.

Measurements taken included 18 characters for mature males, 21 for mature females (Figures 1, 2). These characters comprise two sets, one associated with the carapace or general body form, and another with sexual characters. Measurements for both sexes included:

1. Length of carapace including epistomial spine.
2.* Length of carapace excluding epistomial spine.
3.* Width of carapace including lateral spines.
4.* Width of carapace at base of notch between lateral spine and preceding anterolateral tooth.
5.* Width between tips of outer orbital spines (first anterolateral teeth).
6. Width between tips of suborbital spines.
7. Width between tips of lateral interorbital spines.
8.* Maximum height of body.
9.* Anterior width of metagastric area.
10.* Posterior width of metagastric area.
11.* Length of metagastric area.
12.* Angular (lateral) length of metagastric area.

Measurements of elements in the T-shaped male abdomen included:

13. Greatest width of fused segments 3-5.
14. Median length of fused segments 3-5.
15. Median length of narrow segment 6.
16. Narrowest width of narrow segment 6.
17.* Length of telson.
18.* Width of telson.

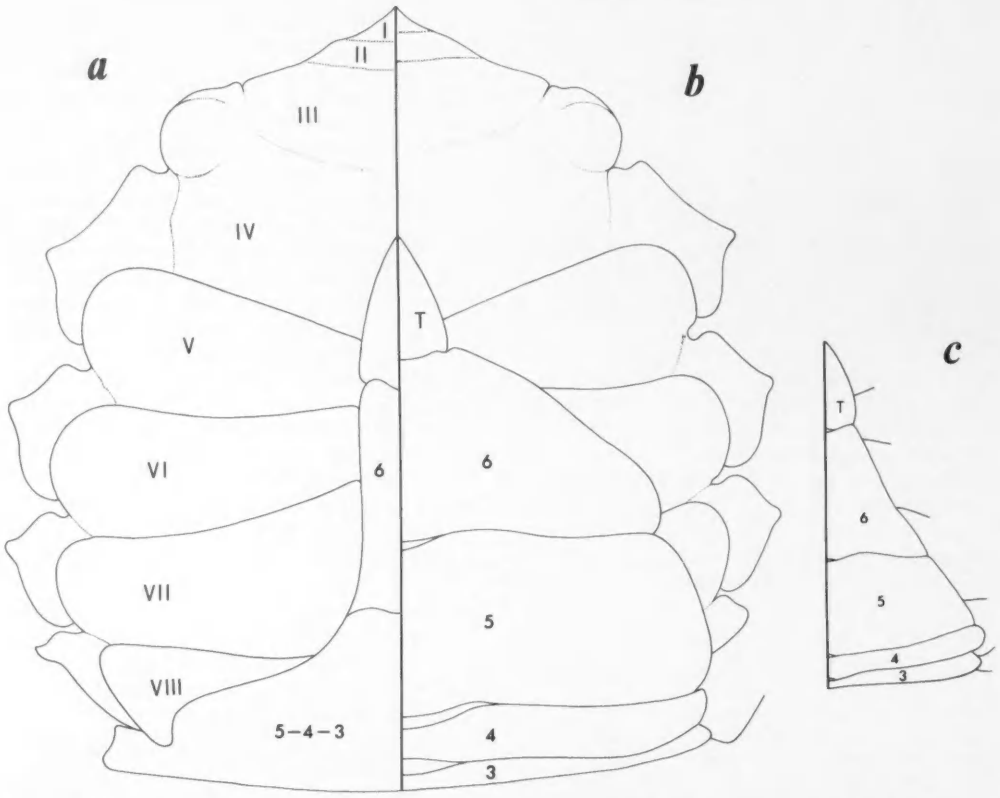


FIGURE 2.—Composite ventral view of thoracic sternites (roman numerals), abdomen (arabic numerals), and telson (T) in situ. **a**, mature male; **b**, mature female; **c**, immature female. Measurements: lengths in midline, widths maximal for structure.

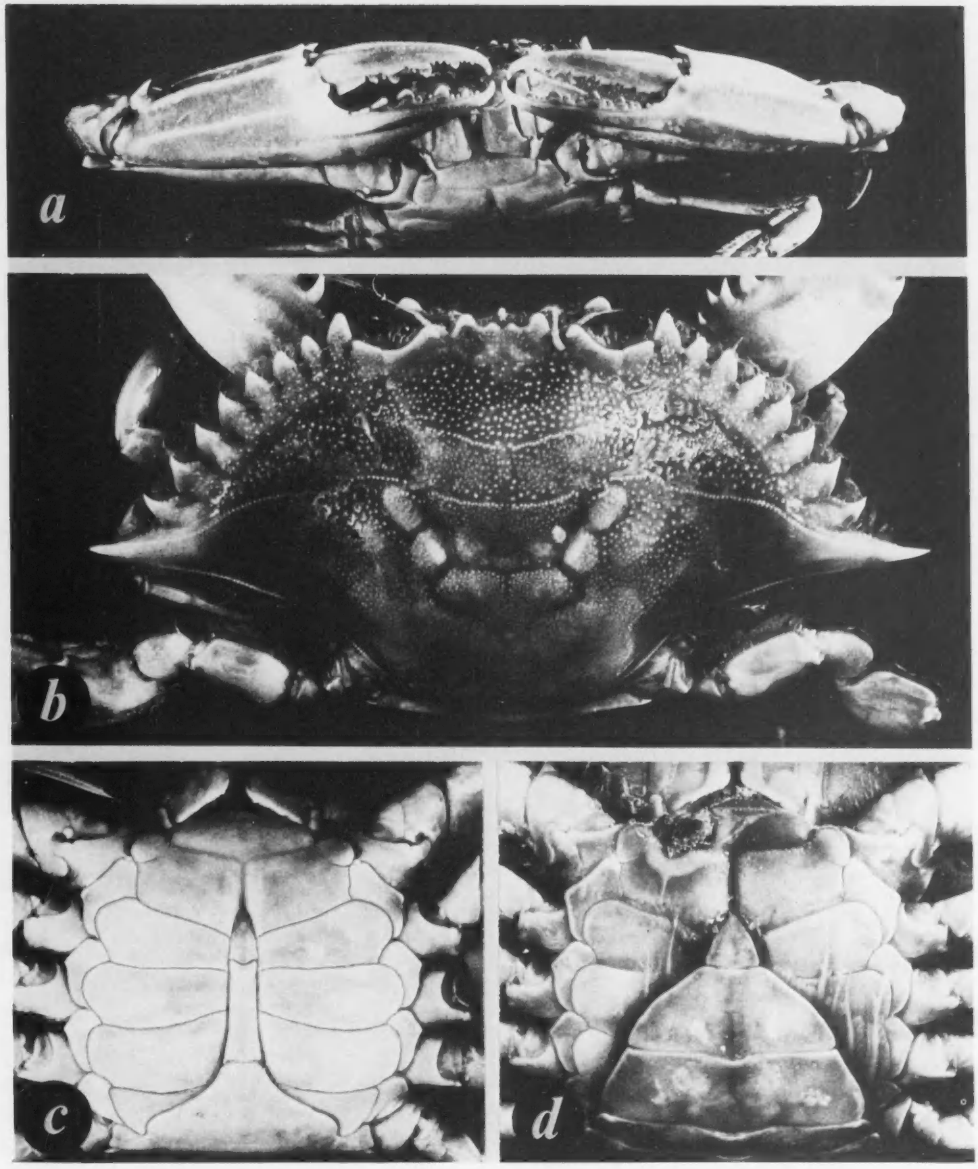


FIGURE 3.—*Callinectes marginatus* (A. Milne Edwards): **a**, chelae in frontal view; **c**, abdomen and sternal area, male, USNM 72351, Salt River Bay, St. Croix, V.I.; **b**, carapace; **d**, abdomen and sternal area, female, USNM 73285, W end San Juan Island near Ft. San Gerónimo, P.R.; **a** × 1; **b** × 1.5; **c** × 1.4; **d** × 1.7.

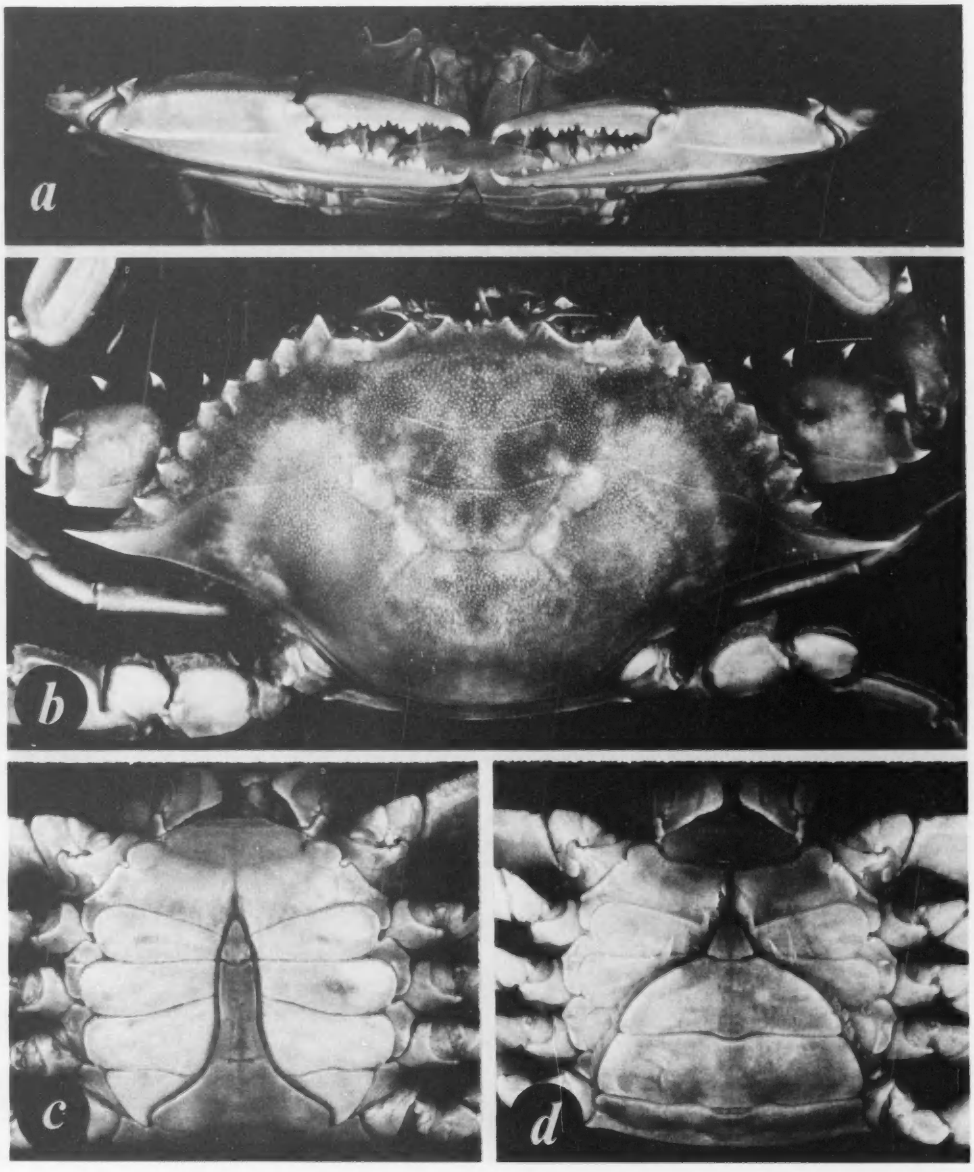


FIGURE 4.—*Callinectes similis* Williams: **a**, chelae in frontal view; **b**, carapace; **c**, abdomen and sternal area, male; **d**, abdomen and sternal area, female; paratypes, UNC-IMS 1556, Beaufort Inlet, Carteret County, N.C.; **a** × 1; **b** × 1.4; **c** × 1.2; **d** × 1.3.

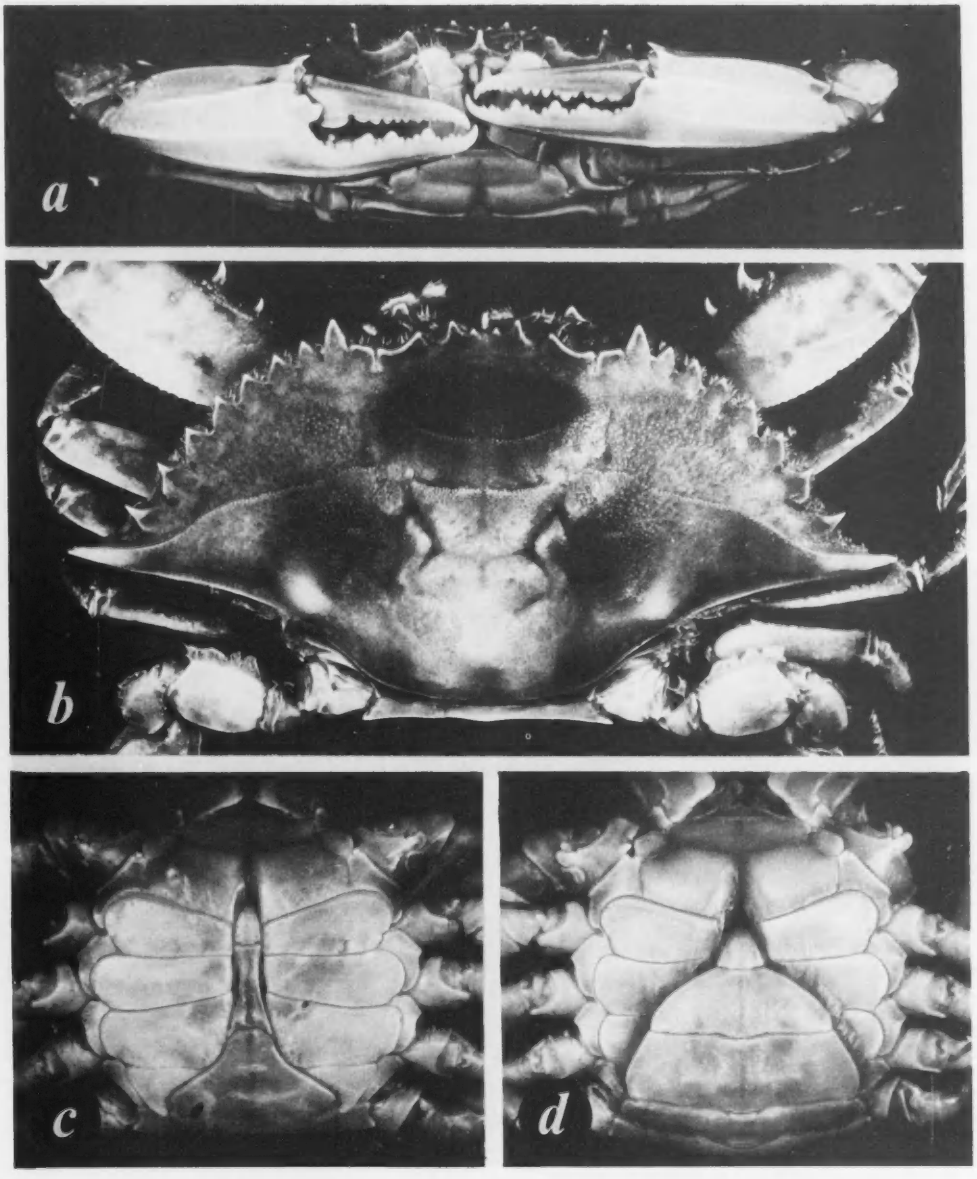


FIGURE 5.—*Callinectes gladiator* Benedict: **a**, chelae in frontal view; **b**, carapace; **c**, abdomen and sternal area, male; **d**, abdomen and sternal area, female, USNM 120940, Nigeria; **a** × 0.9; **b** × 1.4; **c**, **d** × 1.6.

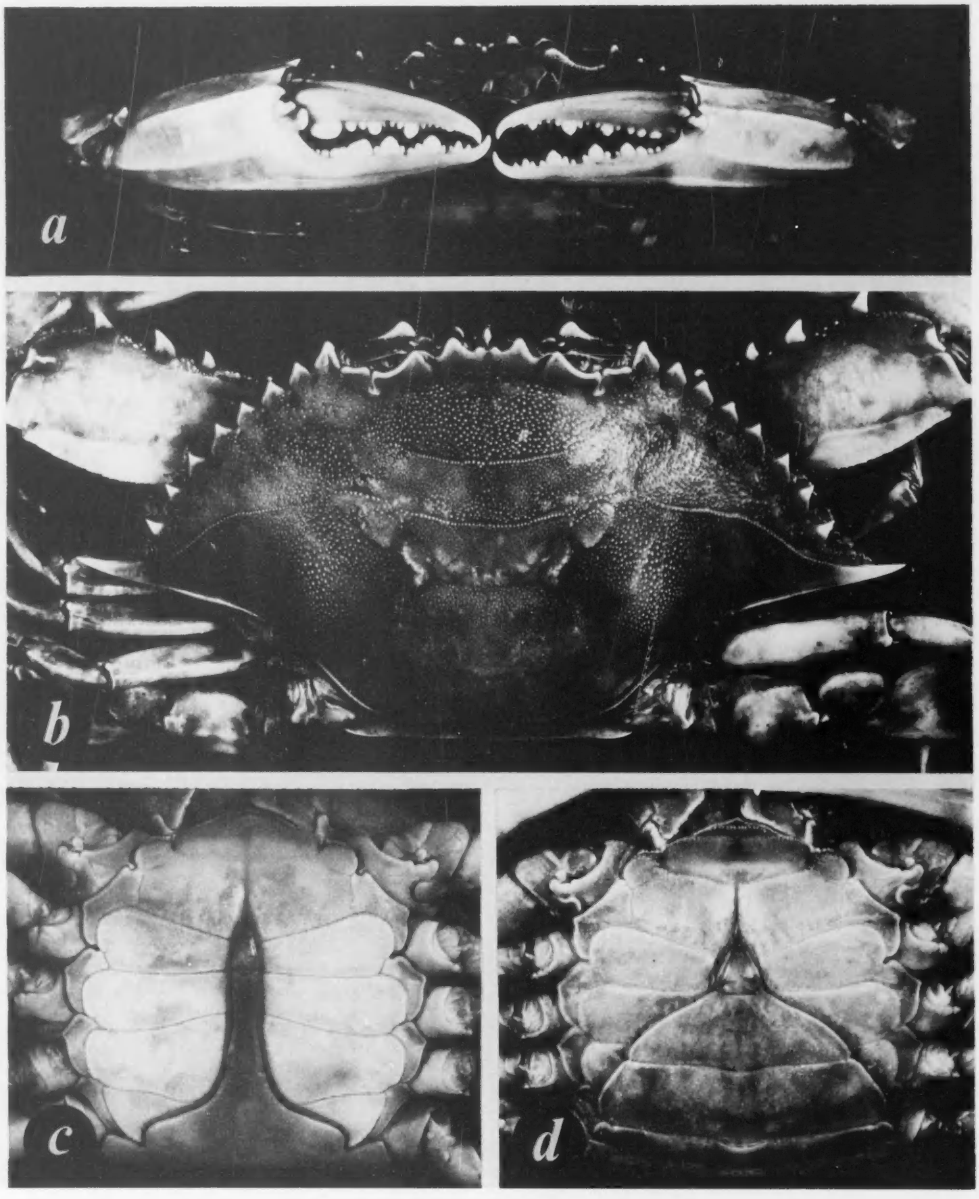


FIGURE 6.—*Callinectes ornatus* Ordway: **a,** chelae in frontal view; **b,** carapace; **c,** abdomen and sternal area, male, 48401, Punta [= Cabo] Cajón, Cuba; **d,** abdomen and sternal area, female, 7584, Curaçao; **a** × 1; **b, d** × 1.3; **c** × 1.5.

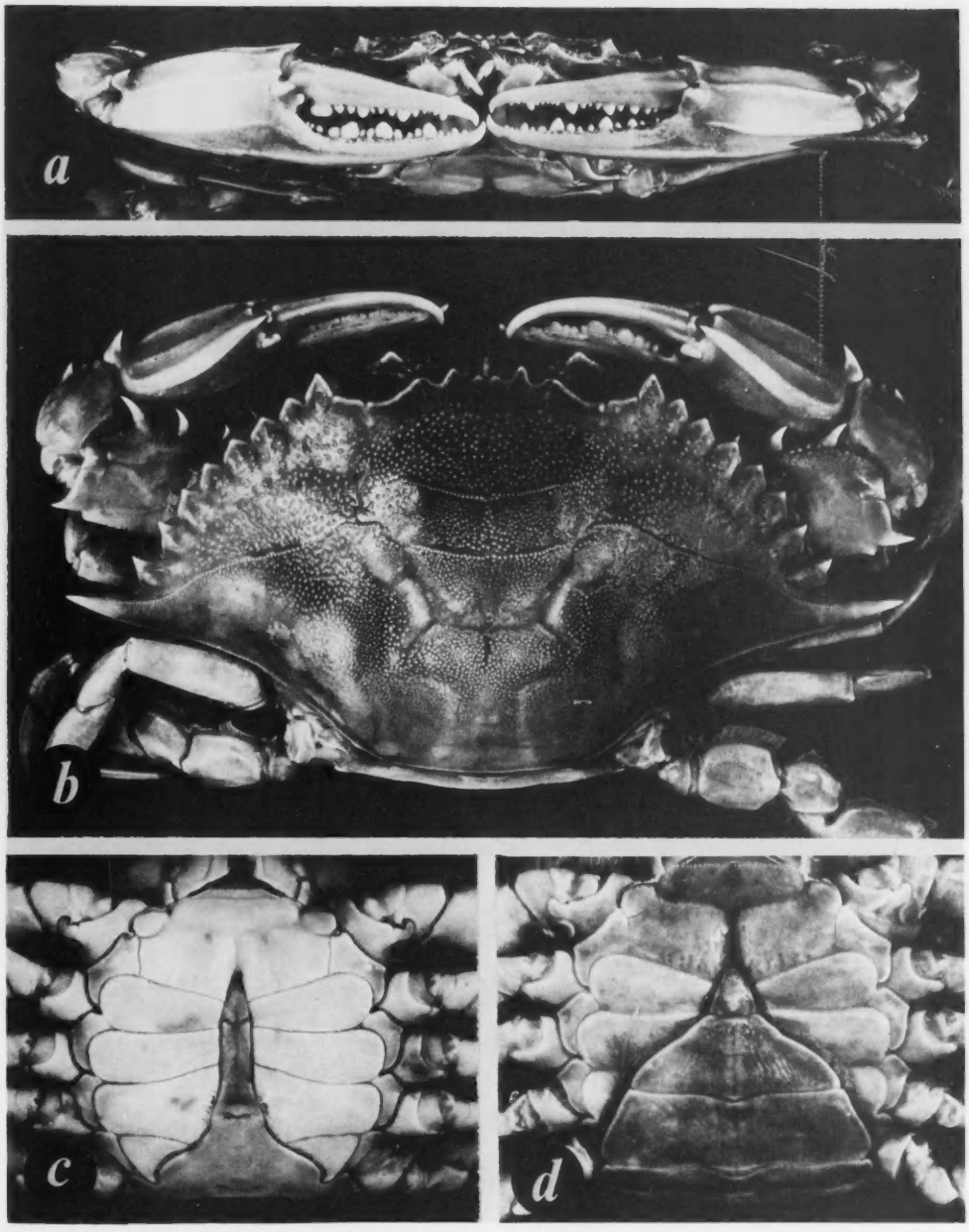


FIGURE 7.—*Callinectes danae* Smith: **a**, chelae in frontal view, male, USNM 60983, São Francisco, Niterói, Brazil; **b**, carapace; **d**, abdomen and sternal area, female, USNM 48400, Los Arroyos, Cuba; **c**, abdomen and sternal area, male, UNC-IMS 2128, Bahía de Mayagüez, P.R.; **a**, **c** × 1; **b** × 1.4; **d** × 1.5.

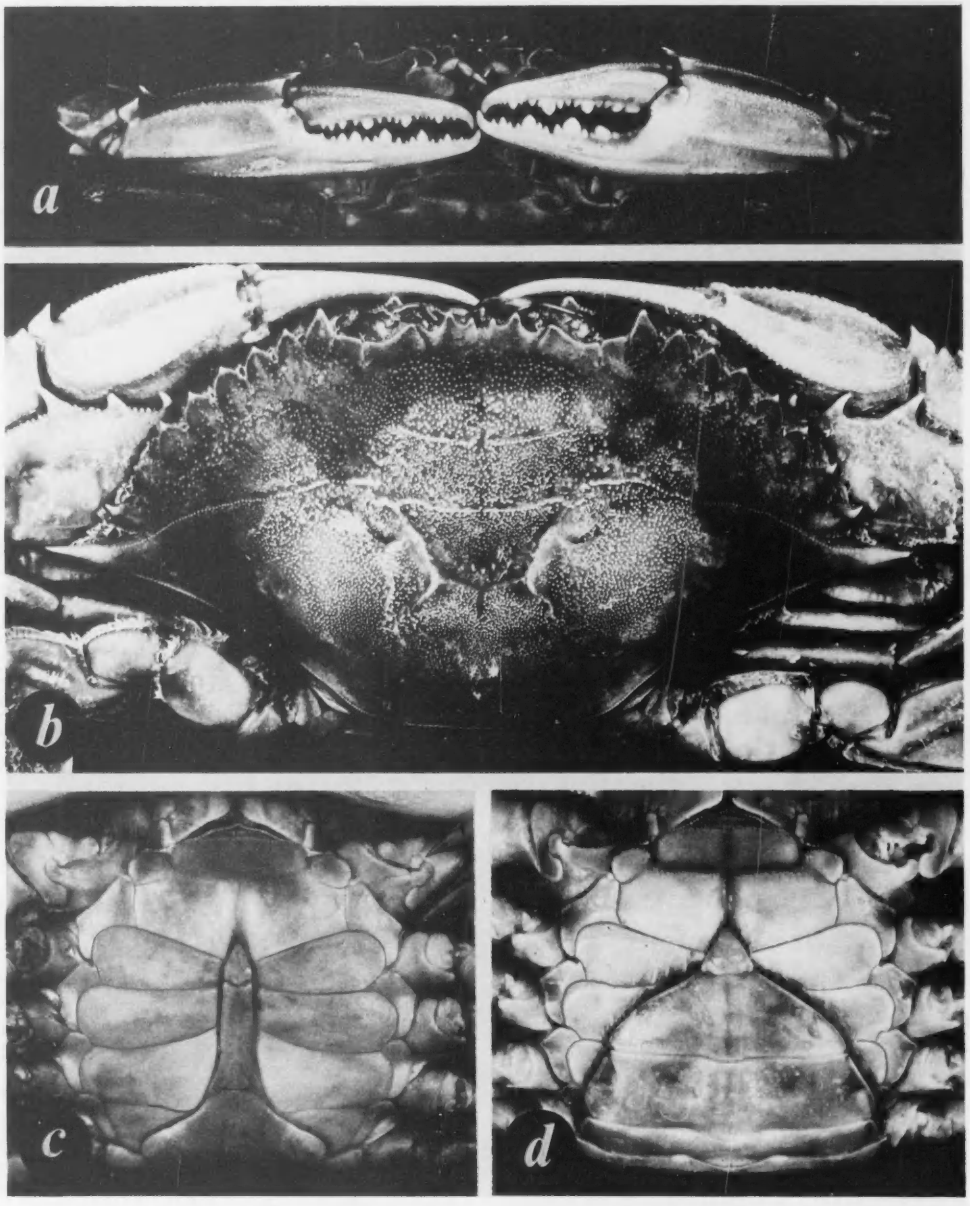


FIGURE 8.—*Callinectes arcuatus* Ordway: **a**, chelae in frontal view; **b**, carapace; **c**, abdomen and sternal area, male, USNM 33417, Isla Magdalena, Baja California, Mexico; **d**, abdomen and sternal area, female, USNM 15431, Estero de los Algodones, SE Guaymas, Sonora, Mexico; **a** × 1; **b**, **c** × 1.2; **d** × 1.4.

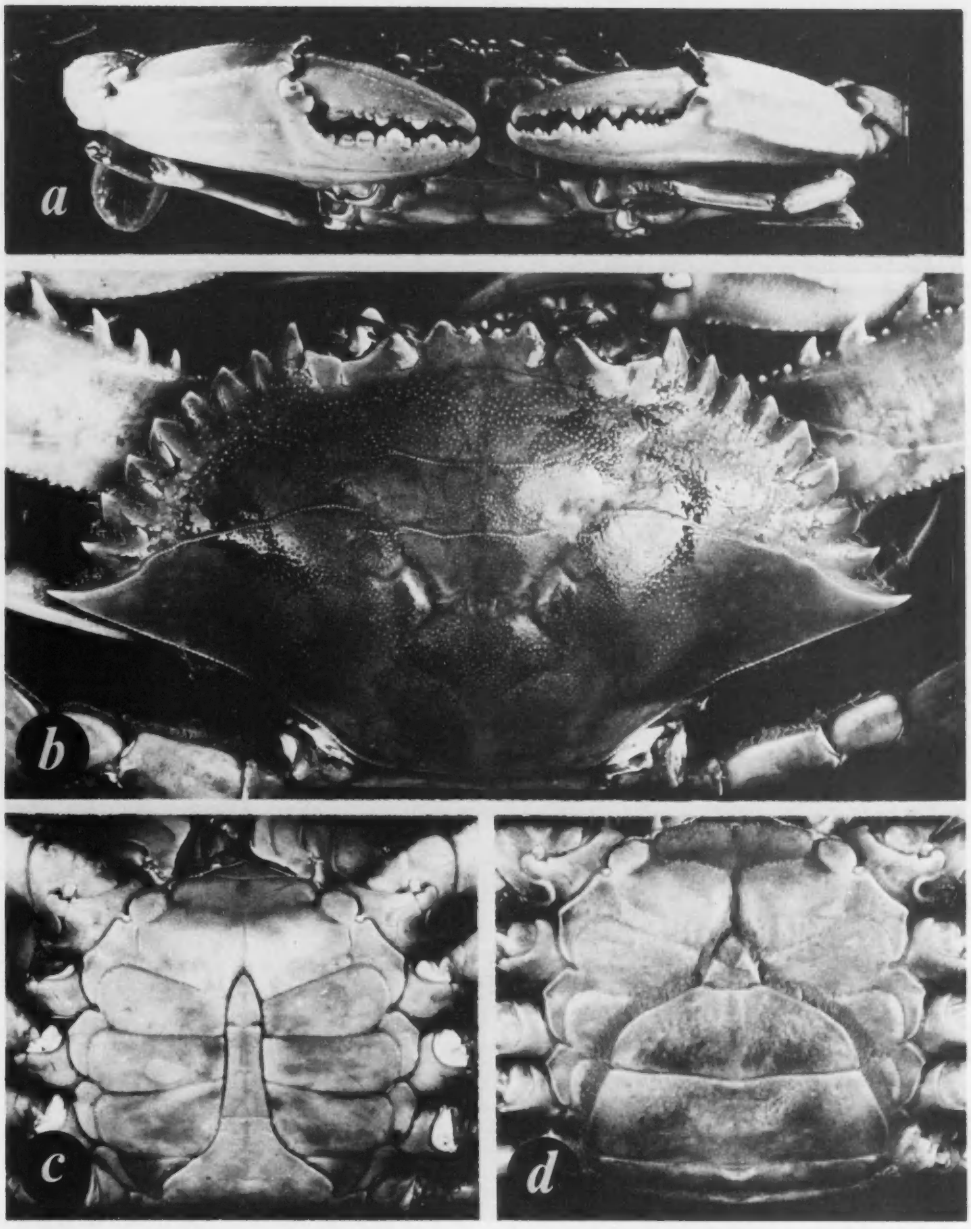


FIGURE 9.—*Callinectes exasperatus* (Gerstaecker): **a**, chelae in frontal view; **b**, carapace; **c**, abdomen and sternal area, male, USNM 19428, Vitória, Estado Espírito Santo, Brazil; **d**, abdomen and sternal area, female, USNM 24467, Puerto Real, P.R.; **a** × 0.8; **b** × 1.1; **c** × 1; **d** × 1.4.

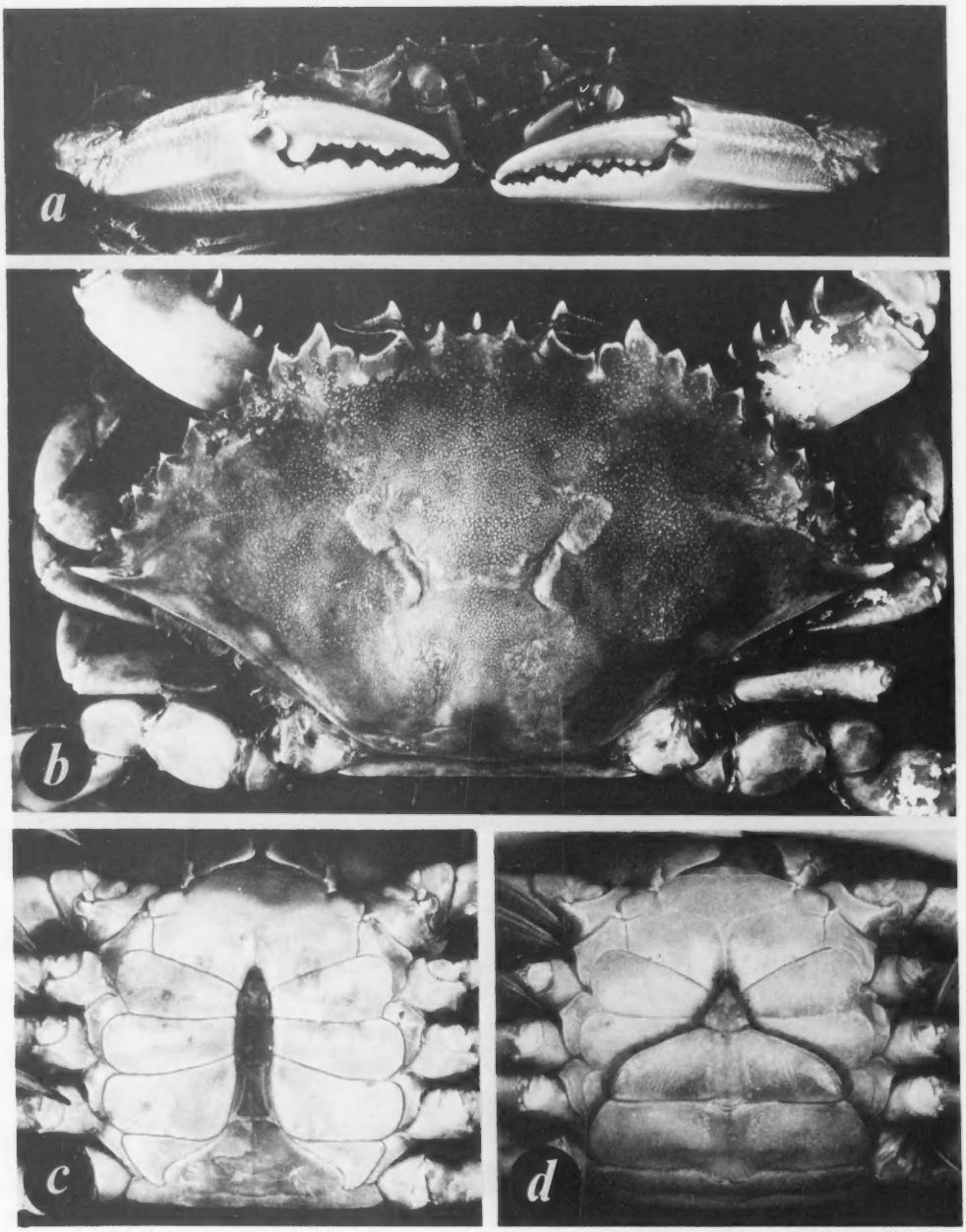


FIGURE 10.—*Callinectes bellicosus* (Stimpson): **a**, chelae in frontal view; **d**, abdomen and sternal area, female, USNM 60010, Pt. Abreojos, Bahía Ballenas, Baja California, Mexico; **b**, carapace; **c**, abdomen and sternal area, male, USNM 15436, La Paz Harbor, Baja California, Mexico; **a**, **c**, **d** × 1; **b** × 1.1.

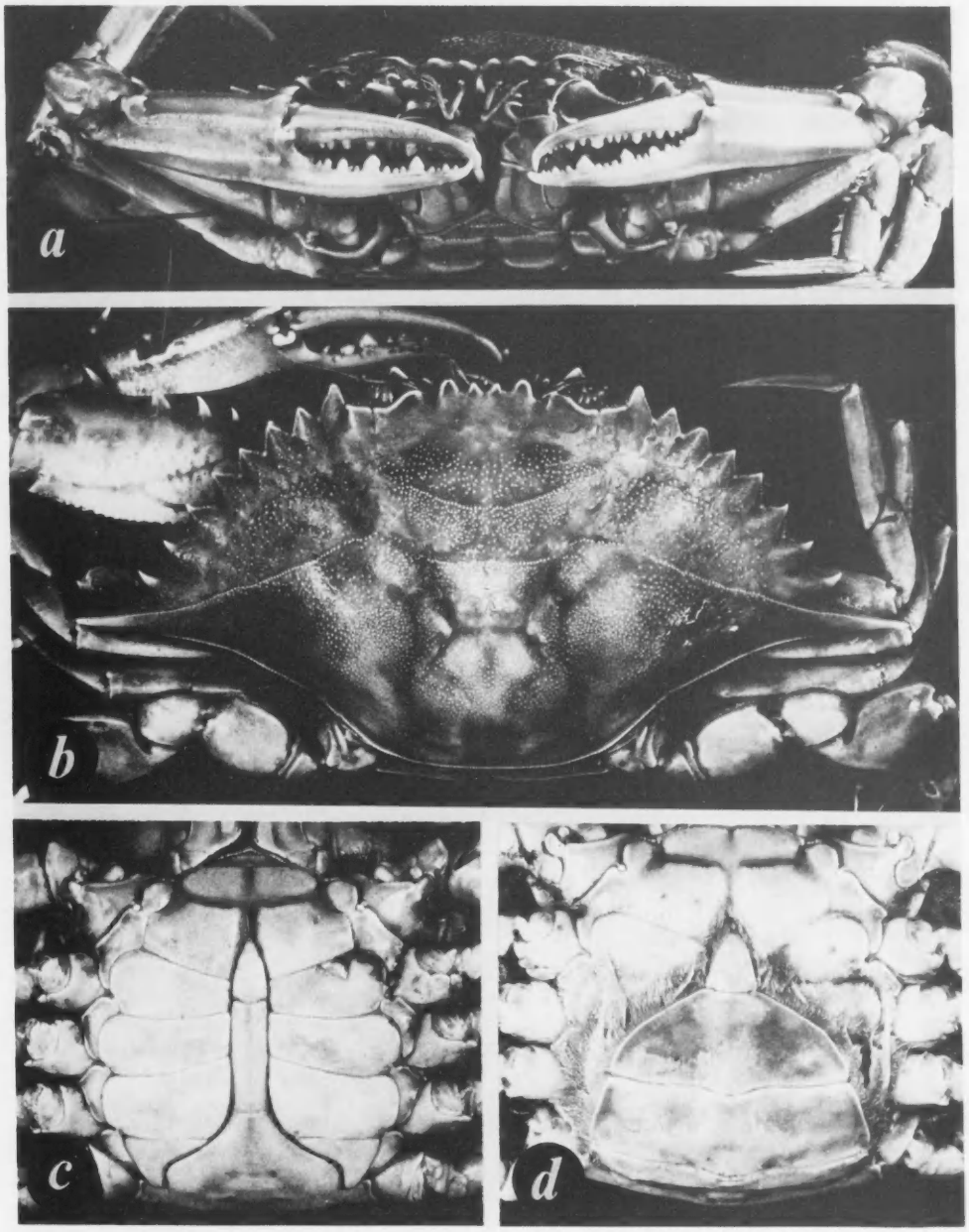


FIGURE 11.—*Callinectes toxotes* Ordway: **a**, chelae in frontal view; **b**, carapace; **c**, abdomen and sternal area, male; **d**, abdomen and sternal area, female, USNM 18507, Acapulco, Guerrero, Mexico; **a** × 1.1; **b** × 0.8; **c**, **d** × 1.

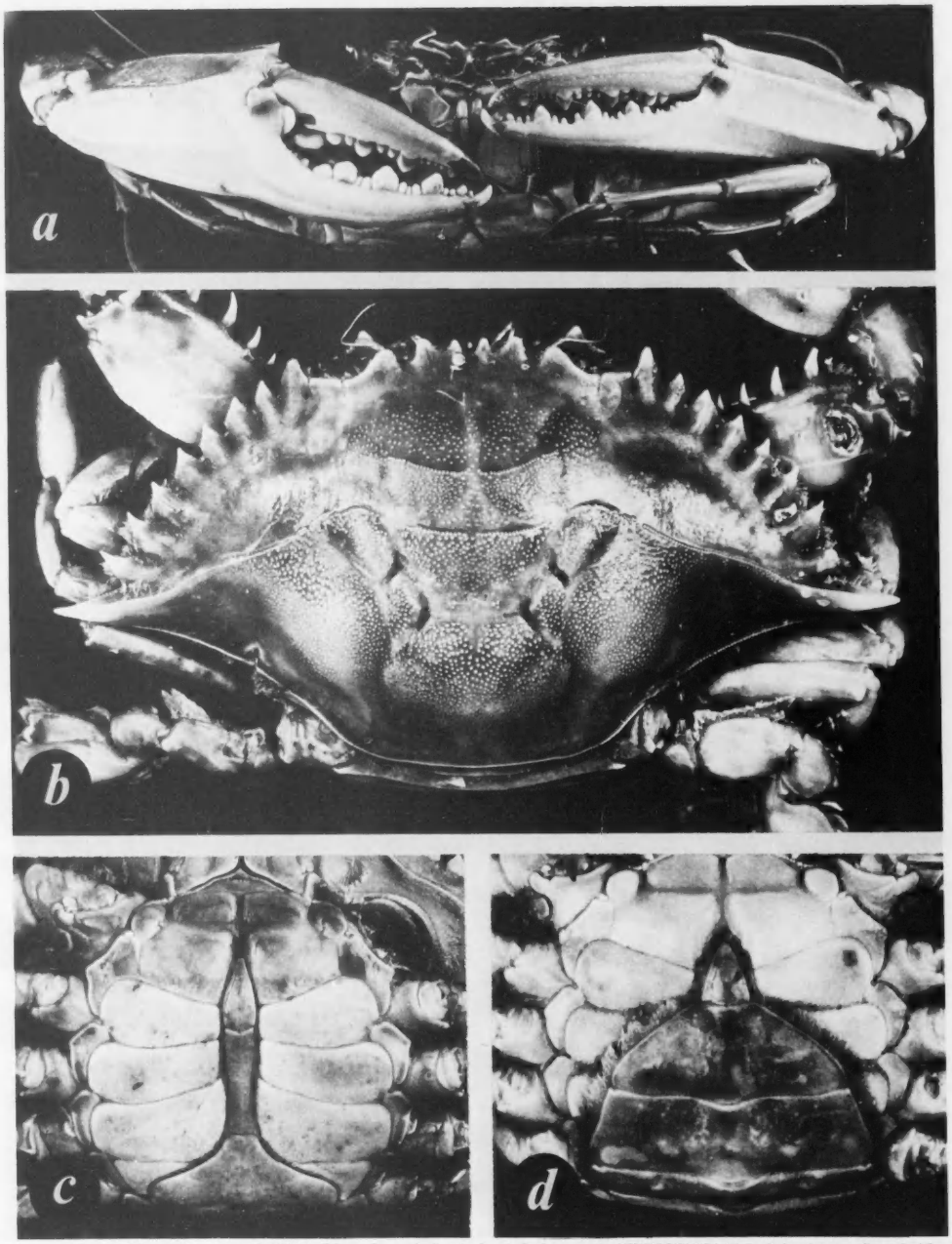


FIGURE 12.—*Callinectes bocourti* A. Milne Edwards: **a**, chelae in frontal view, male, USNM 72354, Fairplain stream above bridge, St. Croix, V.I.; **b**, carapace; **d**, abdomen and sternal area, female, USNM 18235, Sabanilla, Colombia; **c**, abdomen and sternal area, male, USNM 18233, São Luis, Estado Maranhão, Brazil; **a**, **c** × 1; **b** × 1.2; **d** × 1.4.

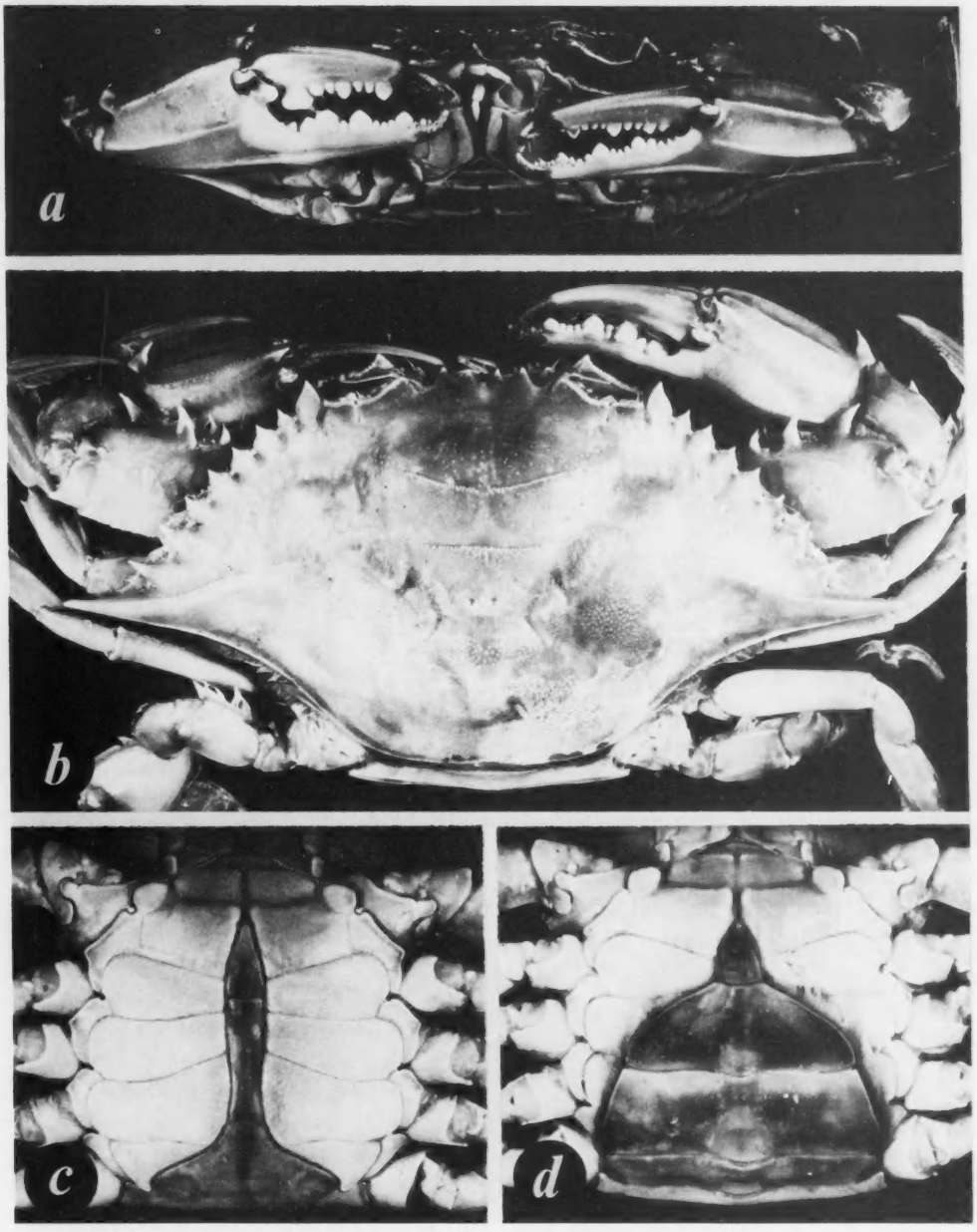


FIGURE 13.—*Callinectes rathbunae* Contreras: **a**, chelae in frontal view; **b**, carapace; **d**, abdomen and sternal area, female; **c**, abdomen and sternal area, male, USNM 122922, Laguna de Alvarado, Veracruz, Mexico; **a**, **b** × 1; **c**, **d** × 1.1.

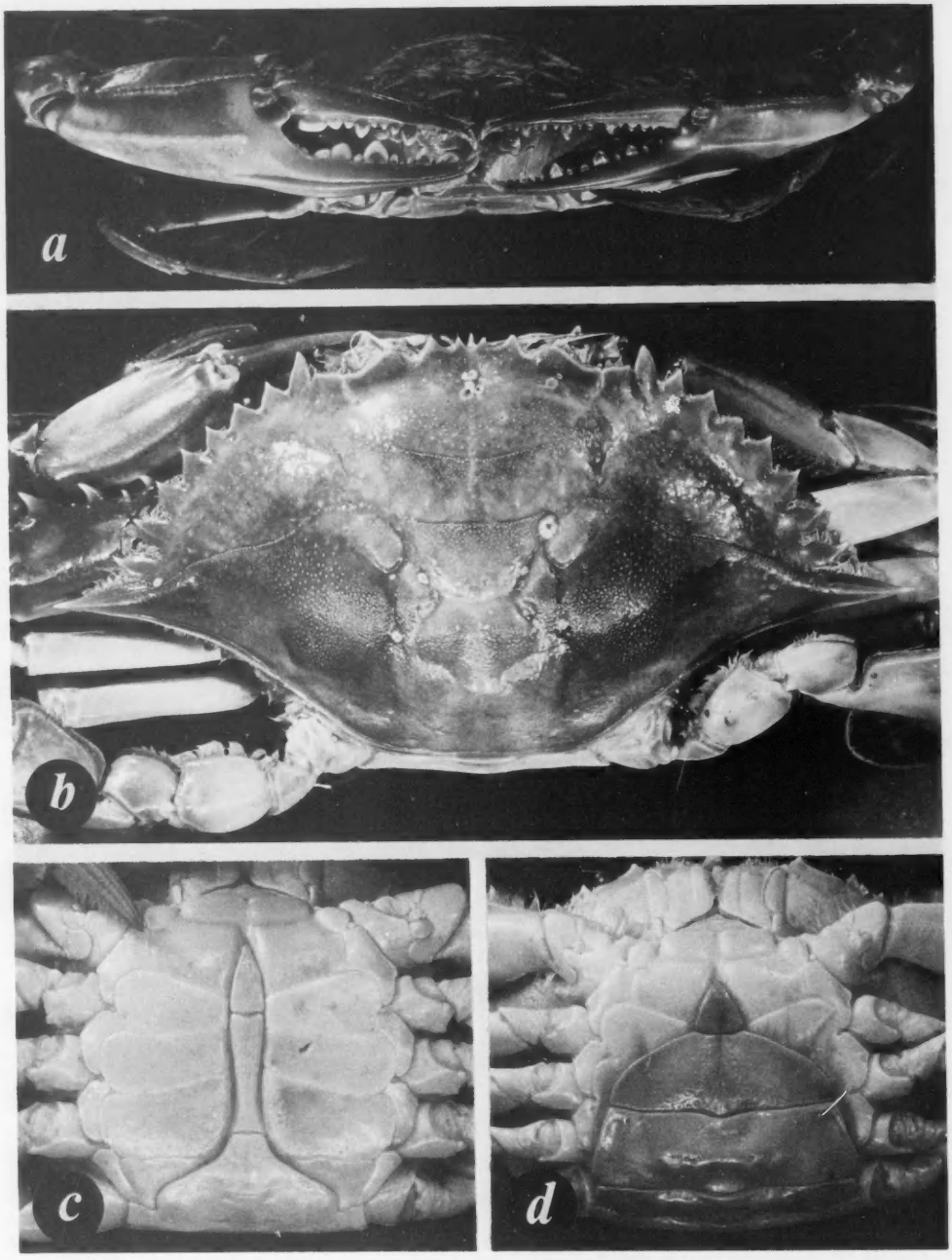


FIGURE 14.—*Callinectes maracaiboensis* Taissoun: **a**, chelae in frontal view, male, USNM 143392, Lago de Maracaibo; **b**, carapace, male, USNM 143393, Puerto Caballo, Maracaibo; **c**, abdomen and sternal area, male; **d**, abdomen and sternal area, female, USNM 139621, Lago de Maracaibo, Venezuela; **a** × 0.95; **b** × 0.85; **c**, **d** × 1.

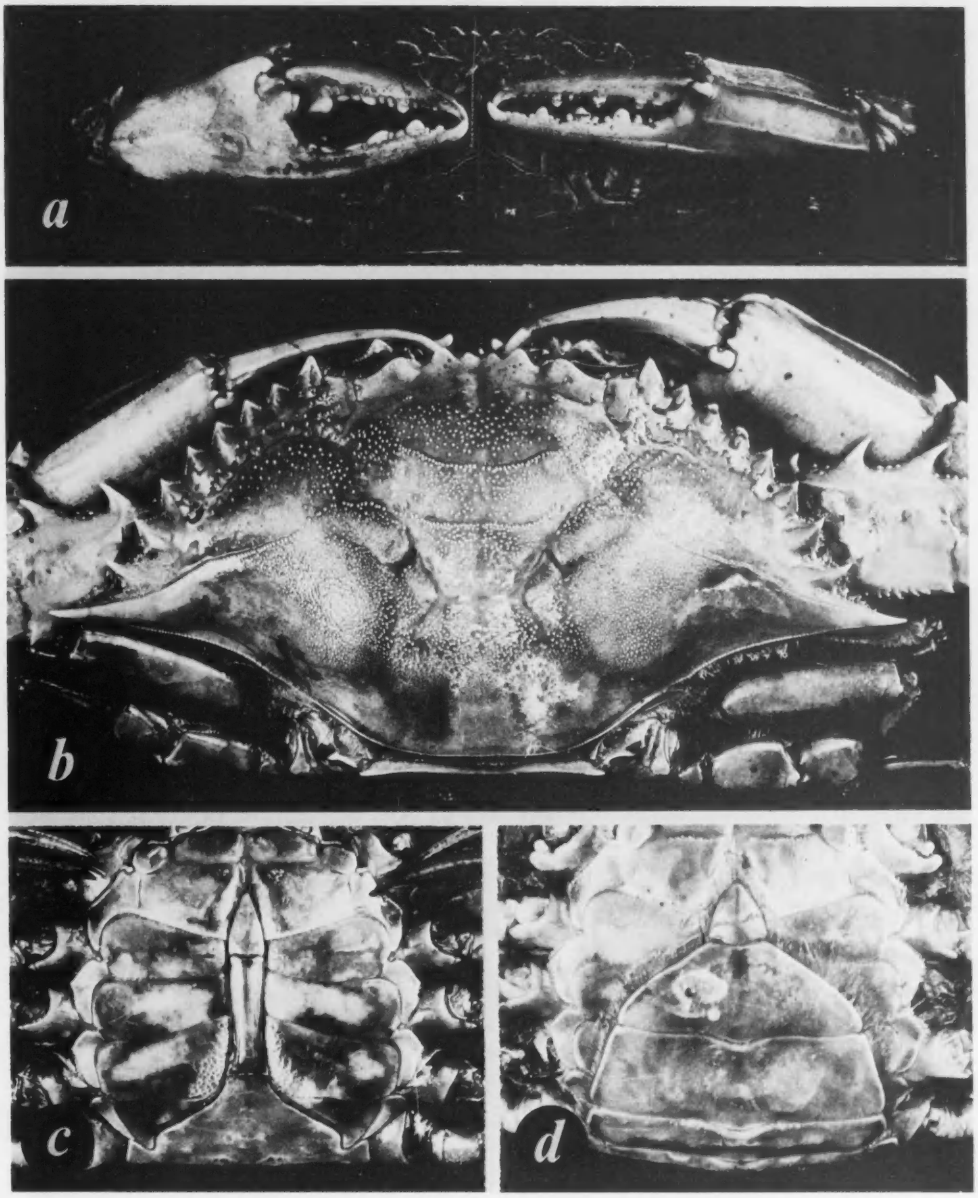


FIGURE 15.—*Callinectes latimanus* Rathbun: **a**, chelae in frontal view; **b**, carapace; **c**, abdomen and sternal area, male; **d**, abdomen and sternal area, female, USNM 54310, Banana, Zaire [= Belgian Congo] **a** × 0.8; **b**, **c** × 1; **d** × 1.9.

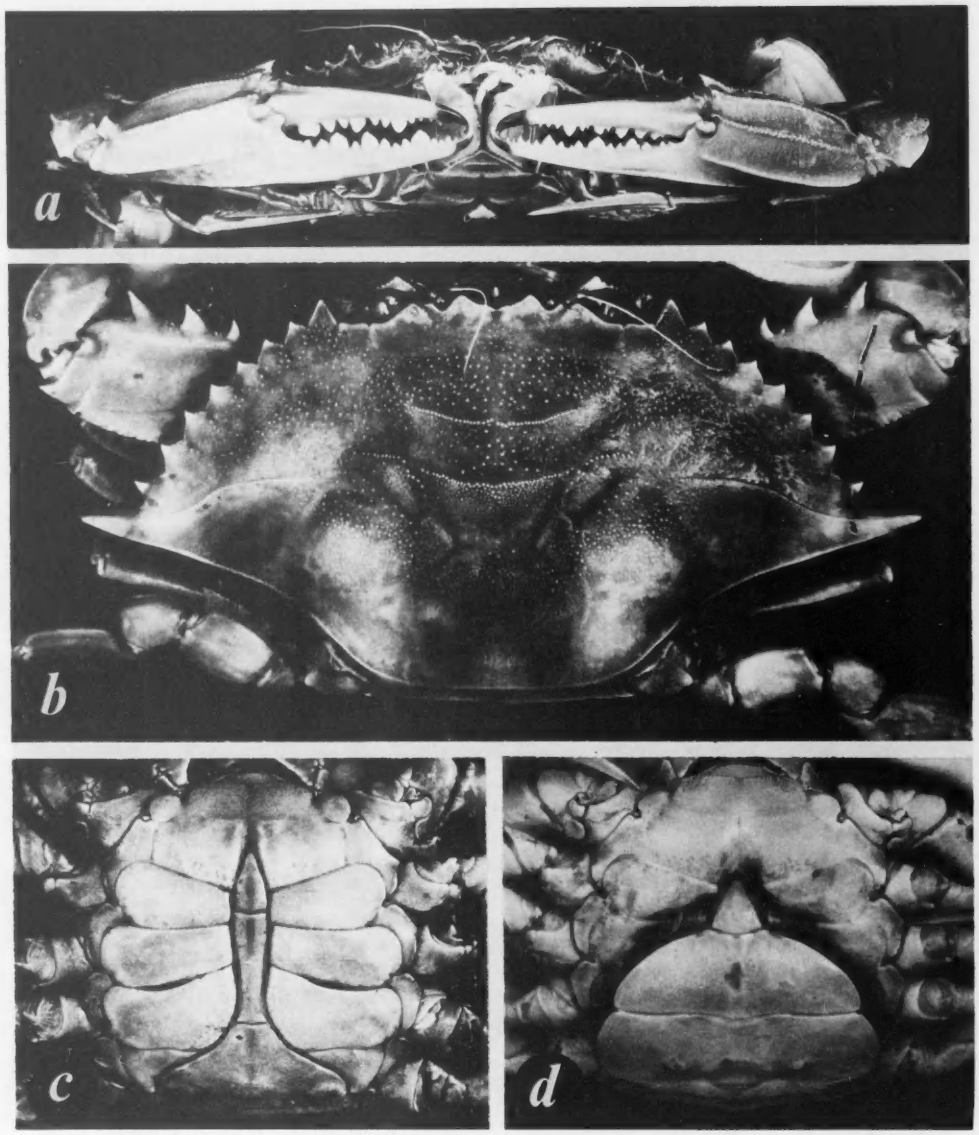


FIGURE 16.—*Callinectes sapidus* Rathbun, forma typica: **a**, chelae in frontal view, male, UNC-IMS 2136, 5 km S Lajas, P.R.; **b**, carapace, male, UNC-IMS 741, North River, Carteret County, N.C.; **c**, abdomen and sternal area, male, USNM 92452, Wye River, Md.; **d**, abdomen and sternal area, female, USNM 30567, Cameron, La.; **a** × 0.8; **b** × 1.3; **c** × 0.6; **d** × 0.85.

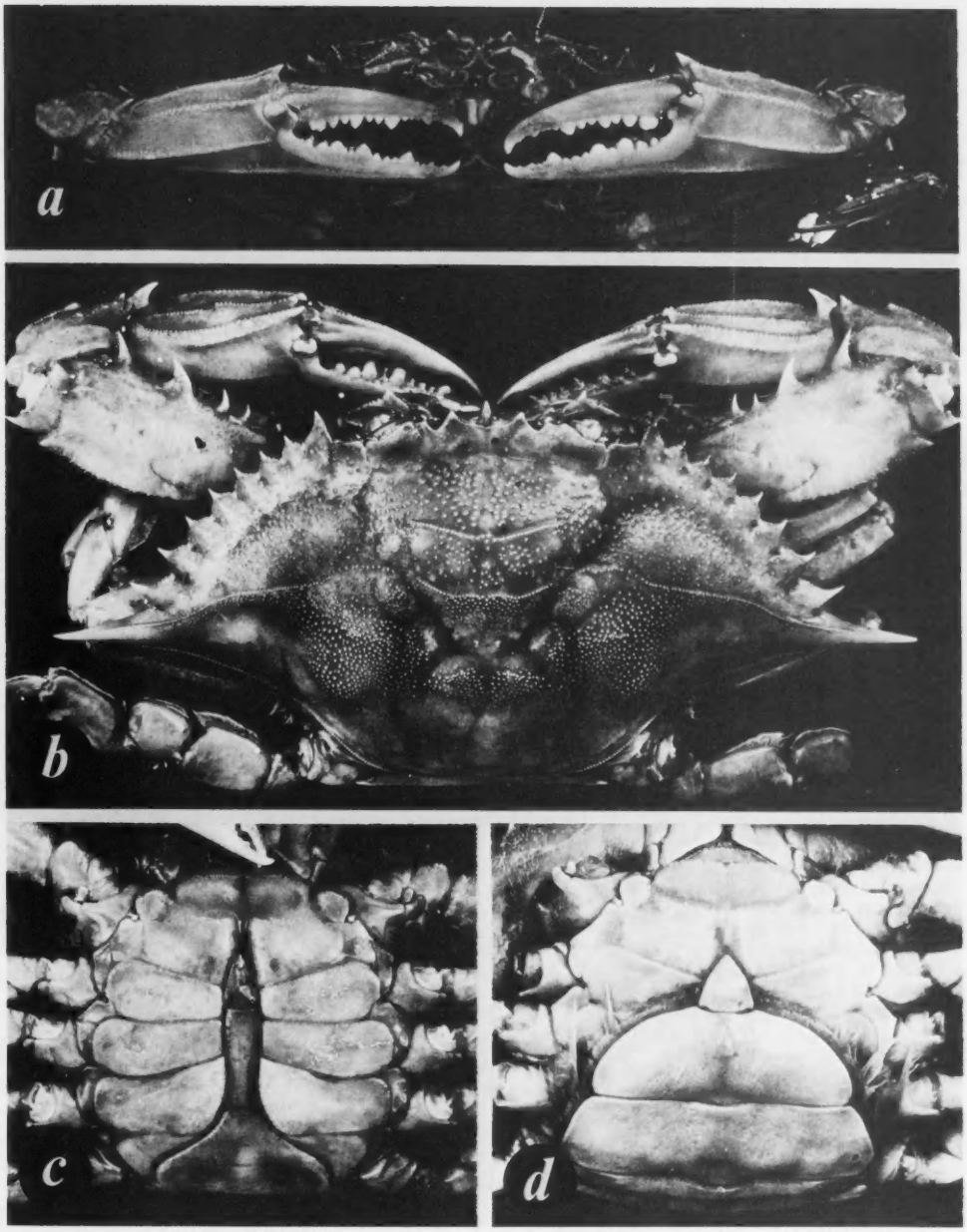


FIGURE 17.—*Callinectes sapidus* Rathbun, forma acutidens: **a,** chelae in frontal view; **b,** carapace; **c,** abdomen and sternal area, male, USNM 18630, Río Escondido, Nicaragua; **d,** abdomen and sternal area, female, USNM 99848, Roca Arroyo Balizas [= Arroyo de Valizes?], Uruguay; **a** × 0.9; **b, c** × 1; **d** × 1.1.

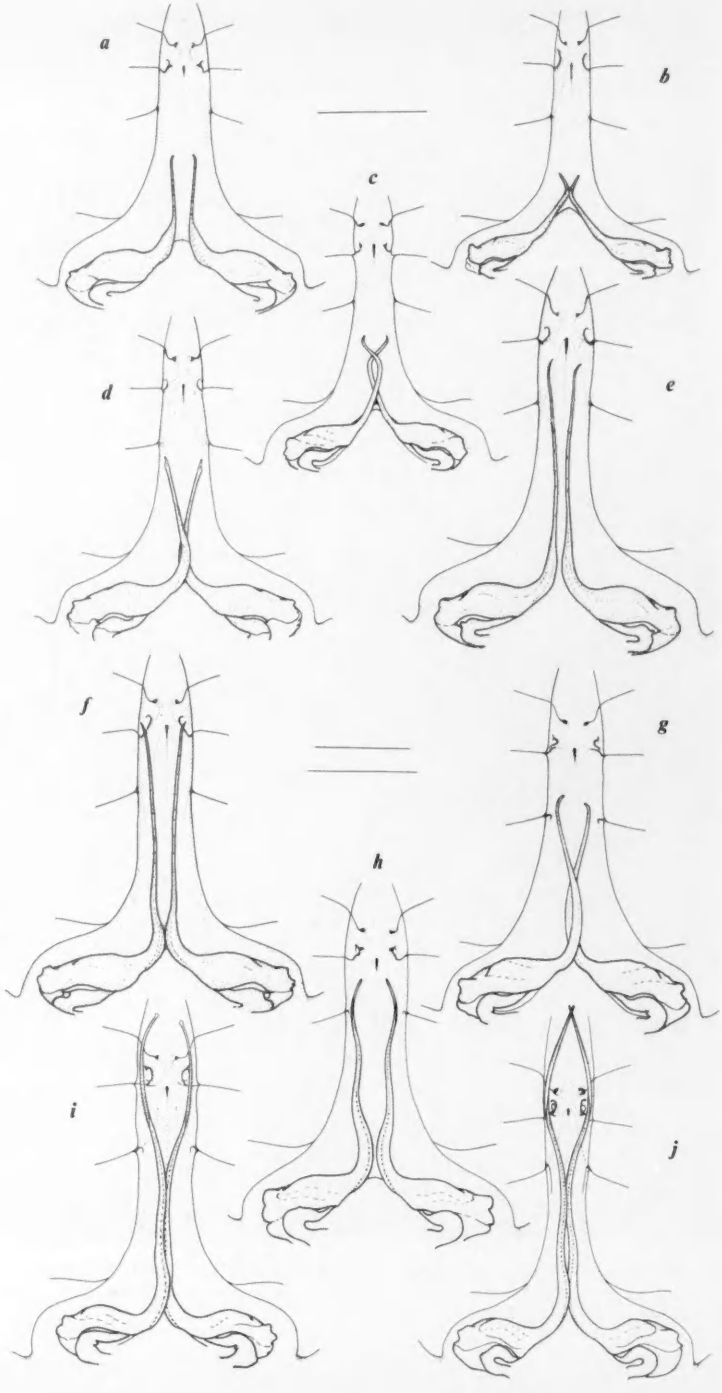


FIGURE 18.—Male, first gonopods in situ with abdomen removed; portions of thoracic sternites IV-VIII: **a**, *Callinectes marginatus* (A. Milne Edwards), USNM 72351, Salt River Bay, St. Croix, V.I.; **b**, *C. similis* Williams, paratype, UNC-IMS 1556, Beaufort Inlet, Carteret County, N.C.; **c**, *C. gladiator* Benedict, Côte du Dahomey, 6°19'N, 2°24'E; **d**, *C. ornatus* Ordway, USNM 48401, Punta [= Cabo] Cajón, Cuba; **e**, *C. danae* Smith, USNM 60983, São Francisco, Niterói, Estado de Rio de Janeiro, Brazil; **f**, *C. arcuatus* Ordway, USNM 33417, Isla Magdalena, Baja California, Mexico; **g**, *C. exasperatus* (Gerstaecker), UNM-IMS 2137, Bahía Fosforescente, P.R.; **h**, *C. bellicosus* (Stimpson), USNM 15436, La Paz Harbor, Baja California, Mexico; **i**, *C. toxotes* Ordway, USNM 18507, Acapulco, Guerrero, Mexico; **j**, *C. bocourti* A. Milne Edwards, USNM 72354, Fairplain stream above bridge, St. Croix, V.I. Scales = 1 cm; **a-f** have higher magnification.

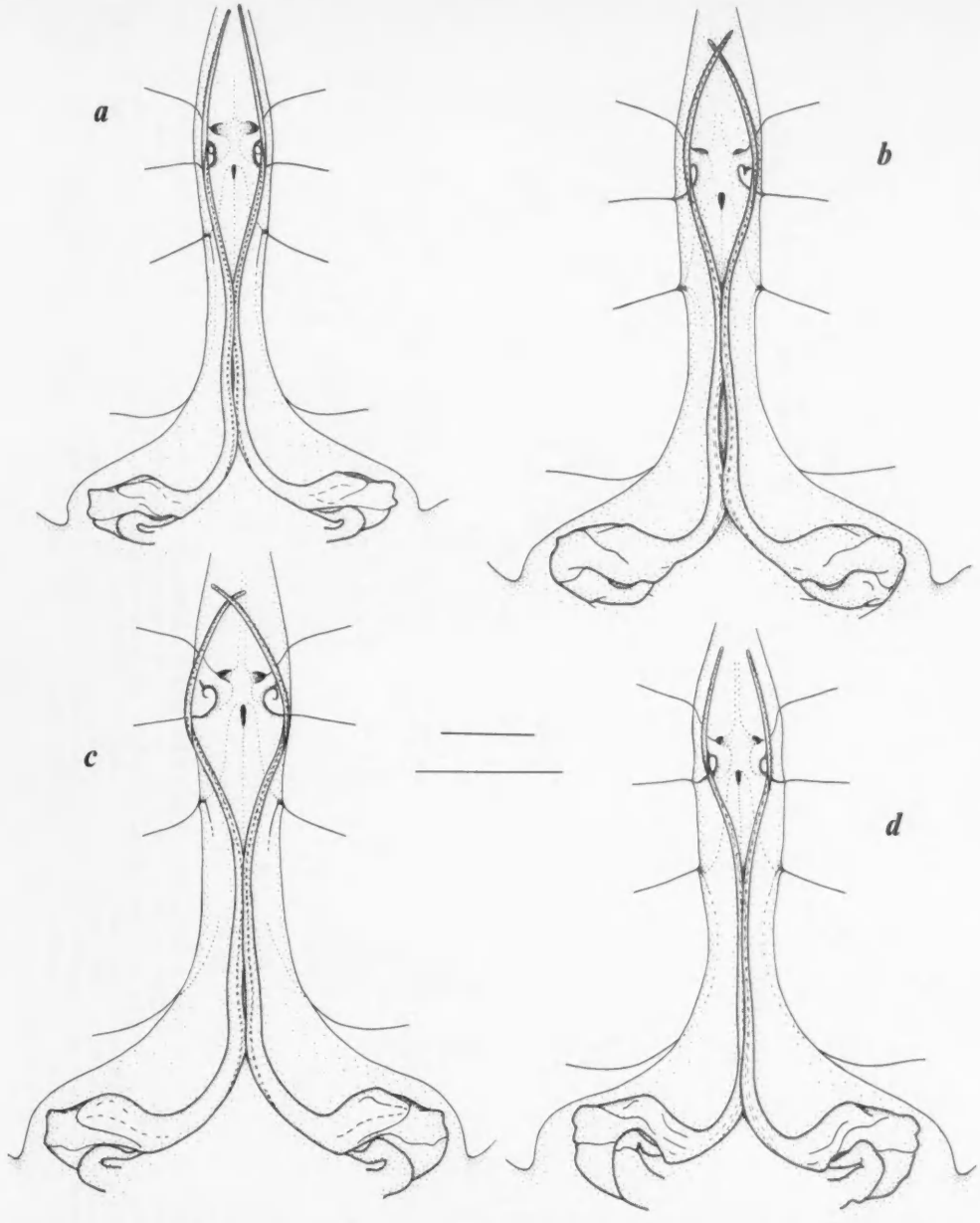


FIGURE 19.—Male, first gonopods in situ with abdomen removed; portions of thoracic sternites IV-VIII; **a**, *Callinectes rathbunae* Contreras, USNM 122922, Laguna de Alvarado, Veracruz, Mexico; **b**, *C. maracaiboensis* Taissoun, Lago de Maracaibo, Venezuela; **c**, *C. latimanus* Rathbun, Plage de Pointe Noire, Congo; **d**, *C. sapidus* Rathbun, USNM 92452, Wye River, Chesapeake Bay, Md. Scales = 1 cm; **d** has lower magnification.

FIGURE 20.—Male, right first gonopod, distal portion in posterior view unless otherwise indicated: **a,** *Callinectes marginatus* (A. Milne Edwards), USNM 72351, Salt River Bay, St. Croix, V.I.; **b,** *C. gladiator* Benedict, Coast of Dahomey, 6°19′N, 2°24′E; **c,** *C. similis* Williams, paratype, UNC-IMS 1556, Beaufort Inlet, Carteret County, N.C.; **d,** *C. ornatus* Ordway, USNM 7584, Curaçao; **e, f,** *C. danae* Smith, USNM 60983, São Francisco, Niterói, Estado de Rio de Janeiro, Brazil; **g, h,** *C. arcuatus* Ordway, USNM 33417, Isla Magdalena, Baja California, Mexico (reconstructed tip of **h** from USNM 60977, Salinas, Ecuador); **i,** *C. exasperatus* (Gerstaecker), UNC-IMS 2137, Bahía Fosforescente, P.R.; **j,** *C. bellicosus* (Stimpson), USNM 15436, La Paz Harbor, Baja California, Mexico; **k,** same, sternal view; **l,** *C. toxotes* Ordway, USNM 18507, Acapulco, Guerrero, Mexico; **m,** *C. bocourti* A. Milne Edwards, USNM 72354, Fairplain stream above bridge, St. Croix, V.I.; **n,** *C. rathbunae* Contreras, USNM 122922, Laguna de Alvarado, Veracruz, Mexico; **o,** *C. maracaiboensis* Taissoun, paratype, USNM 139621, Lago de Maracaibo, Venezuela; **p,** *C. latimanus* Rathbun, Plage de Pointe Noire, Congo. Scales = 1 mm; **a-c** have higher magnification.

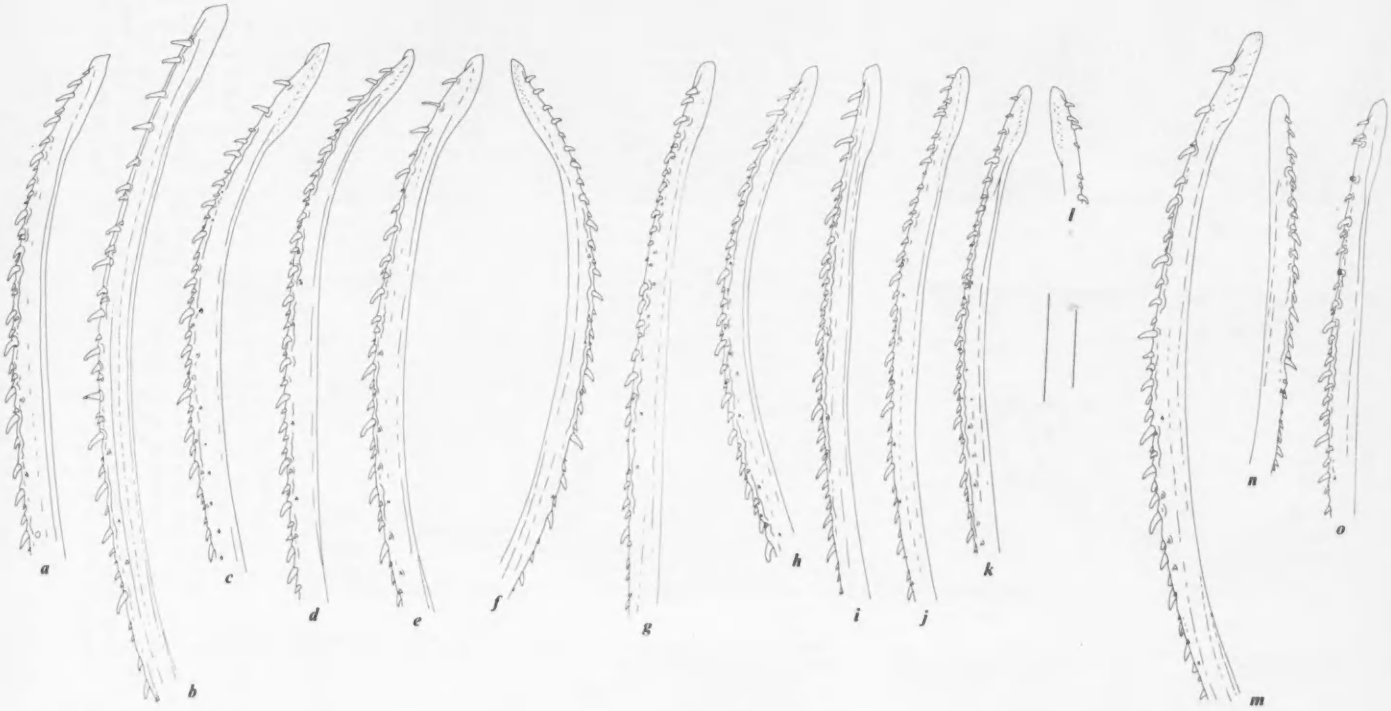


FIGURE 21.—*Callinectes sapidus* Rathbun, male, right first gonopod, distal portion in posterior view unless otherwise indicated: **a**, typical form, USNM 41457, Hudson River at West Point, N.Y.; **b**, typical form, USNM 92452, Wye River, Chesapeake Bay, Md.; **c**, **d**, typical form, USNM 60601, Cape Hatteras, N.C.; **e**, acutidens form, USNM 122944, Deep Lake, Miami, Fla.; **f**, typical form, right first gonopod, USNM 7679, Jamaica; **g**, acutidens form, USNM 72356, Fairplain stream below bridge, St. Croix, V.I.; **h**, acutidens form, USNM 113278, Tortuguero, Costa Rica; **i**, acutidens form, USNM 43921, Mindi Cut, C. Z., Panama; **j**, acutidens form, Lago de Maracaibo, Venezuela; **k**, typical form, USNM 80650, Lago de Maracaibo, Venezuela; **l**, same specimen, right side; **m**, acutidens form, holotype, MCZ 4696, Santa Cruz, Estado de Bahia, Brazil; **n**, acutidens form, paratype, right first gonopod, USNM 19083, Rio de Janeiro, Brazil; **o**, acutidens form, SADZ-B 3234, Praia de Torres, Estado de Rio Grande do Sul, Brazil (tip straightened in preservation). Scales = 1 mm; **a**, **g**, **n** have higher magnification.

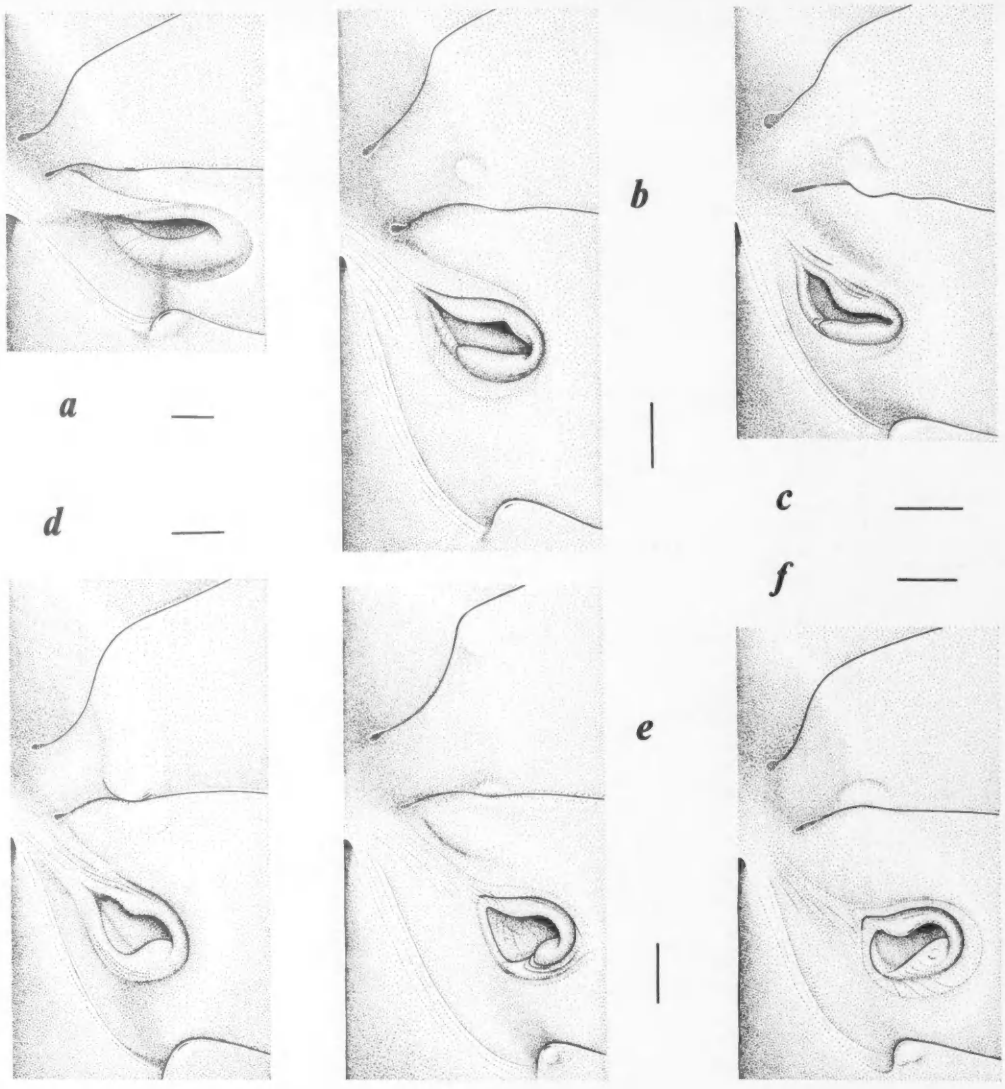
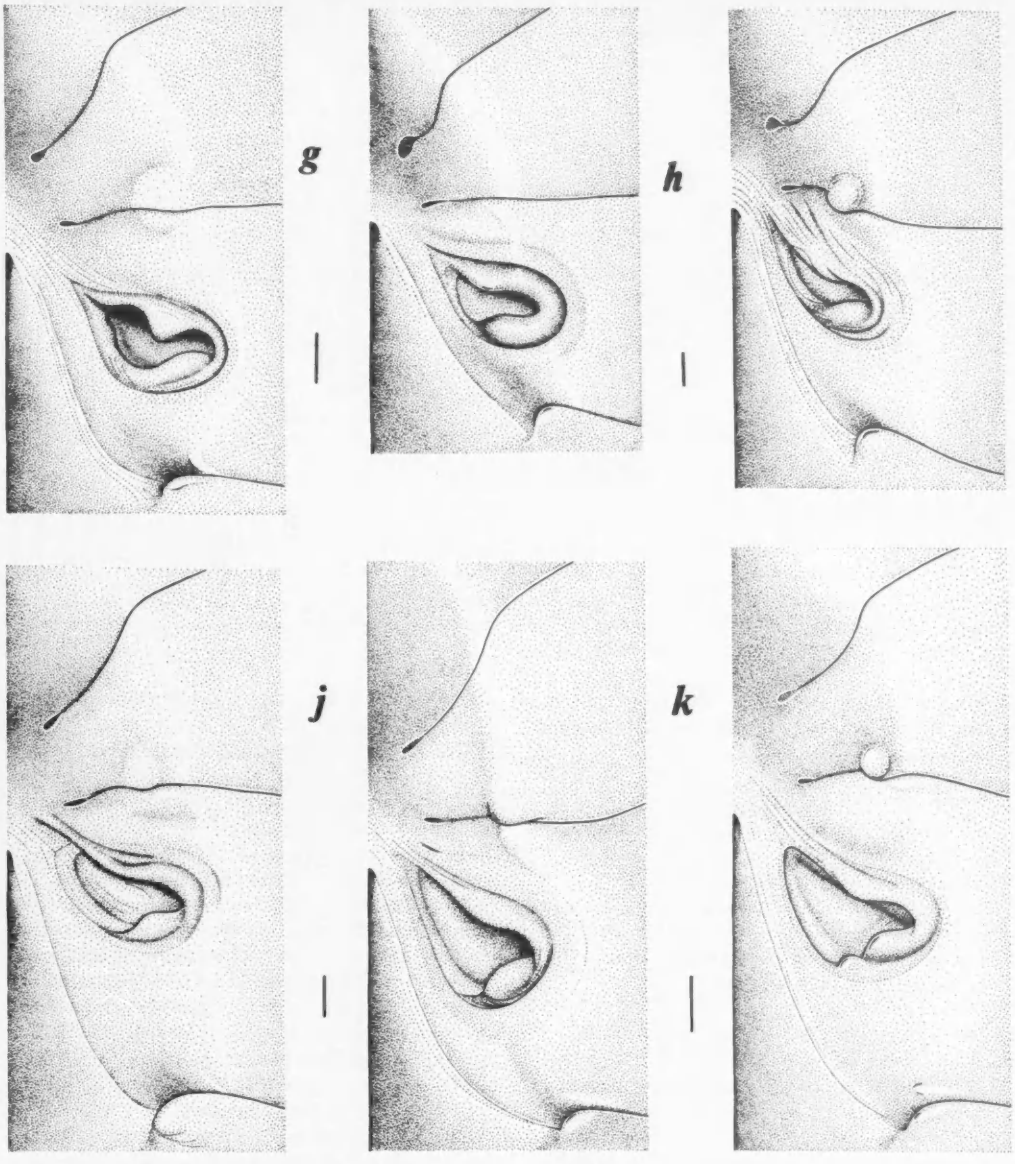


FIGURE 22.—Female, left gonopore and portions of thoracic sternites IV-VII: **a,** *Callinectes similis* Williams, paratype, UNC-IMS 1556, Beaufort inlet, Carteret County, N.C.; **b,** *C. marginatus* (A. Milne Edwards), USNM 73285, W end San Juan I. near Ft. Gerónimo, P.R.; **c,** *C. gladiator* Benedict, Coast of Cameroon, 3°32′N, 9°35′E; **d,** *C. ornatus* Ordway, USNM 7584, Curaçao; **e,** *C. danae* Smith, USNM 60983, São Francisco, Niterói, Estado de Rio de Janeiro, Brazil; **f,** *C. arcuatus* Ordway, USNM 15431, Estero de los Algodones near Guaymas, Sonora, Mexico; **g,** *C. exasperatus* (Gerstaecker), USNM 24467, Puerto Real, P.R.; **h,** *C. bellicosus* (Stimpson), USNM 60010, Pt. Abreojos, Bahía Ballenas, Baja California, Mexico; **i,** *C. toxotes* Ordway, USNM 18507, Acapulco, Guerrero, Mexico; **j,** *C. bocourti* A. Milne Edwards, USNM 18235, Sabanilla, Colombia; **k,** *C. rathbunae* Contreras, USNM 122922, Laguna de Alvarado, Veracruz, Mexico; **l,** *C. maracaiboensis* Taissoun, paratype, USNM 139621, Lago de Maracaibo, Venezuela. Scales = 1 mm.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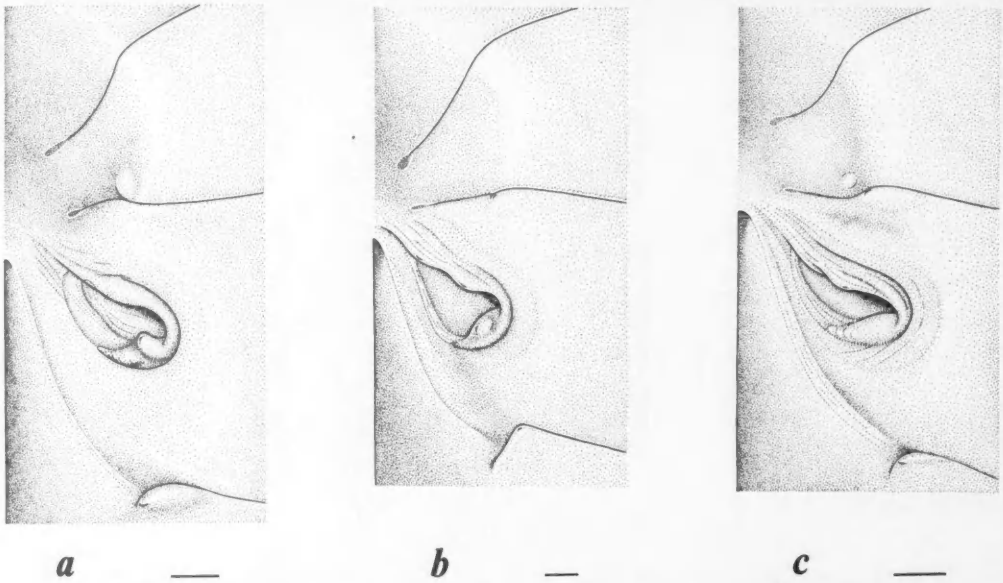

FIGURE 23.—Female, left gonopore and portion of thoracic sternites IV-VII: a, *Callinectes latimanus* Rathbun, Plage de Pointe Noire, Congo; b, *C. sapidus* Rathbun, typical form, USNM 30567, Cameron, La.; c, *C. sapidus* Rathbun, acutidens form, USNM 99848, Roca Arroyo Balizas [= Arroyo de Valizes?], Uruguay. Scales = 1 mm.

Measurements of elements in the broad apron-shaped abdomen of sexually mature females included:

13. Greatest width of segment 2.
14. Greatest width of segment 3.
15. Greatest width of segment 5.
16. Median length of segment 5.
17. Greatest width of segment 6.
18. Median length of segment 6.
19. Median length of segment 3 (proximal edge) to tip of telson.
20.* Length of telson.
21.* Width of telson.

Analysis of selected nonsexual characters.—Study showed that some of these measurements were more valuable than others at the specific level and 11 (marked with asterisks), generally considered useful in verbal description, were chosen for cluster analysis. Unfortunately, they neither clustered as species nor as species groups when analyzed. Results indicated that specific morphological differences in this genus are based on characters other than, or in addition to, those measured and analyzed in this test. Measurements therefore were judged to have limited value in identification.

This finding is supported strongly by evidence other than results of the attempt at cluster analysis. Female *Callinectes* attain sexual maturity in a terminal metamorphic molt. Males attain an adult conformation at sexual maturity but may continue to molt at reduced frequency. Van Engel (1958) and others have shown that *C. sapidus* females molt 18 to 20 times in attaining maturity, males 18 or 19 before becoming mature and 3 or 4 times beyond that stage. The range of variation in number of molts may be much greater than this, for both dwarf and giant sexually mature individuals are known. Allometric changes accentuated at the two ends of this continuum attest to wide variability in form. Estévez (1972) emphasized variability in *C. arcuatus* and *C. toxotes*. Tables 1 and 2 show means, standard deviation, and sample size for selected characters from adult male and female *Callinectes* species. For almost all species the coefficient of variation ($V = 100s/x$) is high for all characters shown, an indication that morphometrically there is great variation in the group. Simpson, Roe, and Lewontin (1960:91) stated that V values greater than 10

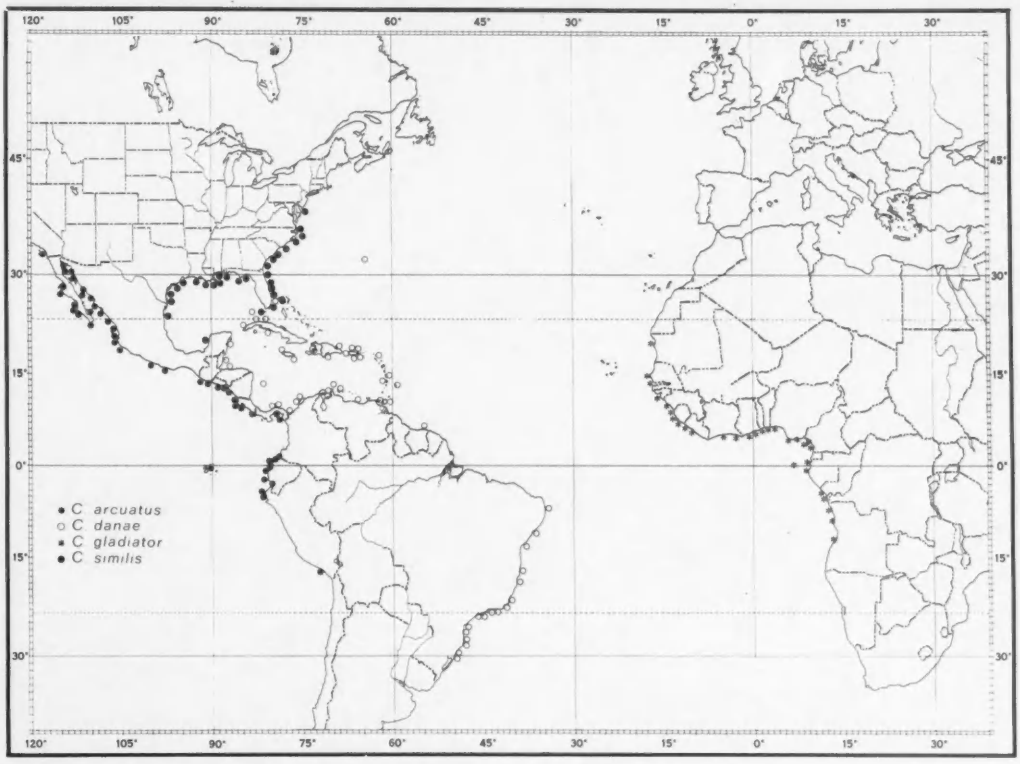

FIGURE 24.—Respective geographic distributions of *Callinectes arcuatus* Ordway, *C. danae* Smith, *C. gladiator* Benedict, and *C. similis* Williams in the Atlantic and eastern Pacific oceans based on specimens studied and verified published records.

indicate that a sample is not reasonably unified. Throughout the genus great variation in morphometry of the body makes keys for identification involving proportions almost impossible to devise unless qualified by exceptions.

From a different viewpoint, Stephenson et al. (1968) applied methods of numerical analysis to 44 species and putative subspecies of *Portunus* (mainly from America, but certain Indo-Pacific species for comparison), *Callinectes, Arenaeus,* and *Scylla,* relying on presence or absence of 57 characters to build up a data matrix from which character assessments could be made. The method nicely demonstrates that *Callinectes* is a very homogeneous group, but the internal relationships implied do not correspond harmoniously with classical interpretation. This is not a matter of conflict, but simply one of judgment, the method seeming to be limited by interpretation of character states, weighting being one serious problem and choice of characters another. Were the analysis run with different emphases, results might reflect those to some extent.

LARVAL DEVELOPMENT

Among *Callinectes* species, larval development of only *C. sapidus* and *C. similis* has been determined by hatching eggs and rearing in the laboratory. Costlow, Rees, and Bookhout (1959) and Costlow and Bookhout (1959) described seven zoeal stages, atypically an eighth, and a megalopa for *C. sapidus.* Larvae and megalopae of the two species are apparently almost identical, the stages being similar to those of other portunids (Costlow and Bookhout, pers. commun.). Importantly, the megalopae of *Callinectes* lack an internal carpal spine on the chelipeds whereas megalopae of *Portunus* have a well-developed spine on this member

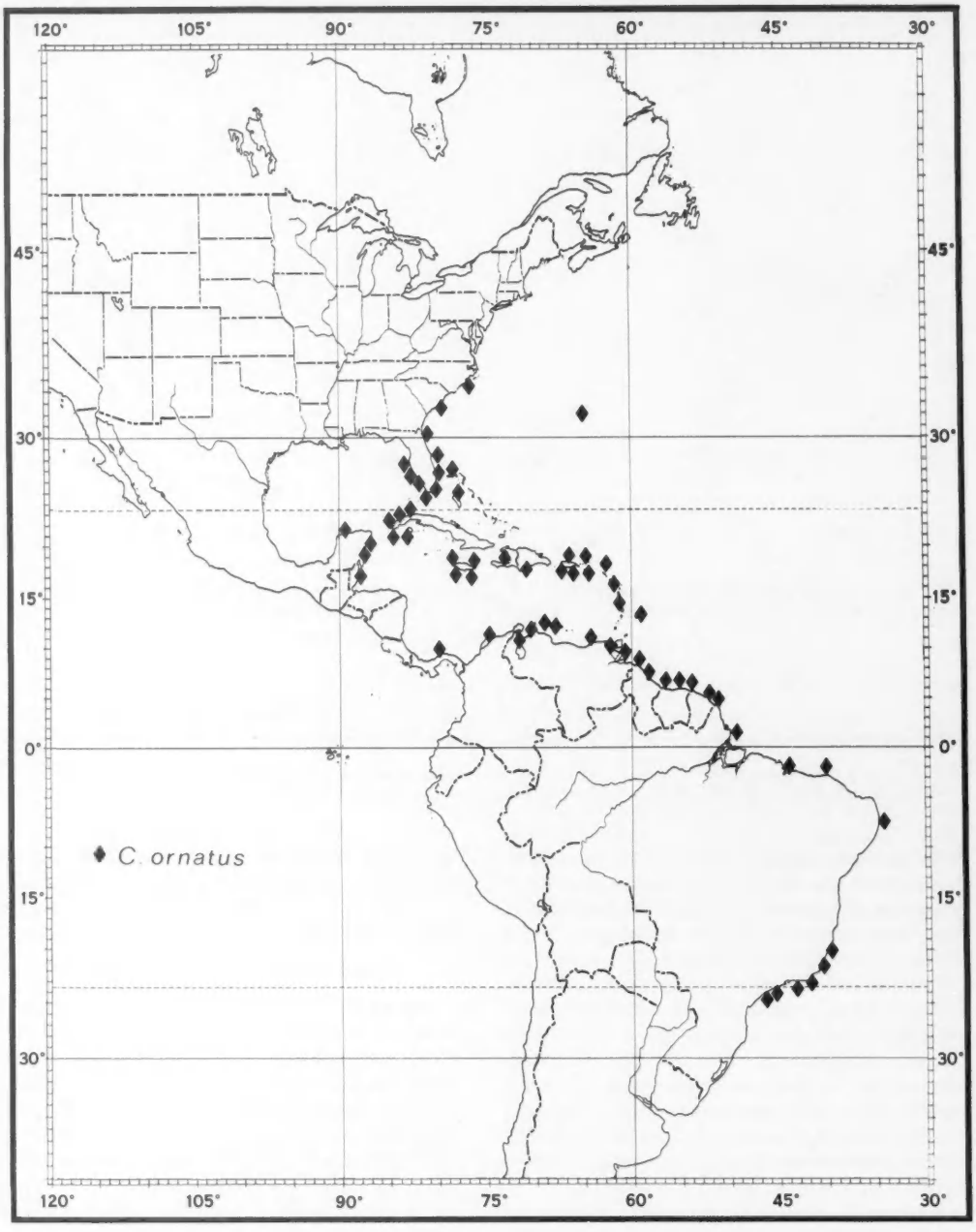

FIGURE 25.—Geographic distribution of *Callinectes ornatus* Ordway in the western Atlantic Ocean based on specimens studied and verified published records.

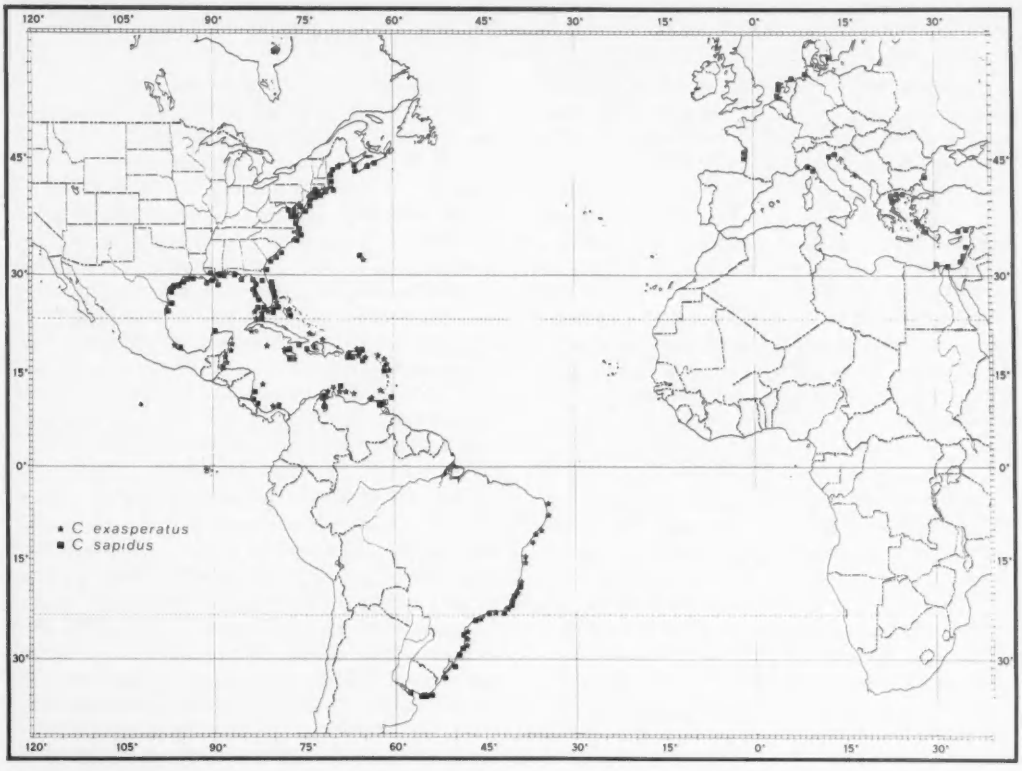

FIGURE 26.—Respective geographic distributions of *Callinectes exasperatus* (Gerstaecker) and *C. sapidus* Rathbun in the western Atlantic Ocean with introductions to the eastern Atlantic and Mediterranean Sea, based on specimens studied and verified published records.

(Williams, 1971), showing one of the generic distinctions at an early phase of development.

Costlow (1965, 1967) followed the early work on larvae with a series of experimental studies showing that development of *C. sapidus* is subject to variation both in staging and duration. Total development time of *C. sapidus* from hatching of egg to transformation of the megalopa to first crab stage has varied from 31 to 69 days in the laboratory in various combinations of salinity and temperature, but duration of individual stages is variable even in a single salinity-temperature combination. The stages are constant enough, however, that Van Engel (1958), Cargo (1960), Nichols and Keney (1963), Pinschmidt (1964), Tagatz (1968), More (1969), and Williams (1971) were able to identify zoeae or megalopae from nearshore oceanic and estuarine plankton. In nature as in experiments, development time may be extended by environmental conditions. Megalopae have been found throughout the year in North Carolina estuaries.

FOSSIL RECORD

Hard parts of portunids most abundant as fossils in Tertiary formations in eastern North and Middle America are portions of the chelipeds, usually the dactyls and portions of the propodi. Some deposits contain remains of carapaces and/or sterna, occasionally almost whole exoskeletons of crabs, but any of the remains are scarce. It was largely on the basis of cheliped fragments that Rathbun (1919a, b, 1926, 1935) listed and described *Callinectes* species from formations attributed to ages as old as the Oligocene. Withers (1924) described a fragment of chela from the Eocene of Jamaica as *Callinectes,* and Blake (1953) added information

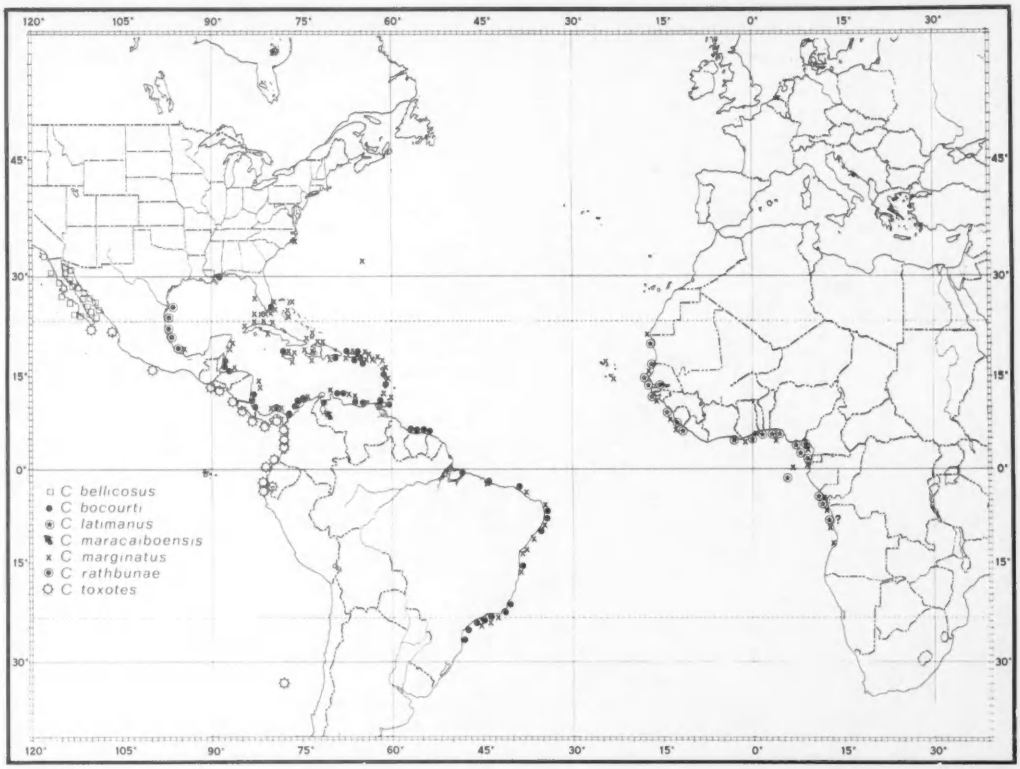

FIGURE 27.—Respective geographic distributions of *Callinectes bellicosus* Stimpson, *C. bocourti* A. Milne Edwards, *C. latimanus* Rathbun, *C. marginatus* (A. Milne Edwards), *C. maracaiboensis* Taissoun, *C. rathbunae* Contreras, and *C. toxotes* Ordway in the Atlantic and eastern Pacific oceans based on specimens studied and verified published records.

on remains from the Quarternary. Williams (1965) uncritically accepted determinations for Atlantic and Gulf Coastal Plain records from the Miocene to Recent, but study of this material, even though its interpretation is beyond the scope of the present paper, leads to an attitude of restraint.

The characters by which *Callinectes* is distinguished from other portunid genera, shape of male abdomen and lack of an internal carpal spine on the chelipeds, are rarely evident in the fossil material, the only undoubted specimens (treated in species accounts below) coming mainly from Pleistocene and a few Miocene horizons. All others studied lack characters for positive first order identification and therefore their determinations rest on secondary features such as shape of the chelae or other nondiagnostic parts of the body. Although the numerous cheliped fragments most resemble these parts in living species of *Callinectes,* they also resemble those of *Ovalipes* and certain *Portunus,* especially the large *P. pelagicus* and *P. sanguinolentus* distributed widely in the Indo-Pacific region today (Stephenson, 1962), as well as the robust *Arenaeus cribrarius* and *A. mexicana,* respectively from Atlantic and Pacific shores of the Western Hemisphere (Rathbun, 1930). A single propodal finger of a form attributed to *P. sayi* reported from the Miocene of Florida (Rathbun, 1935) greatly resembles other remains attributed to *Callinectes.* Margins of warmer seas of early and mid Tertiary (Ekman, 1953; Hazel, 1971) could have favored such forms or others like contemporary *Scylla* of Indo-Pacific waters, fossil representatives of which were described [=?] by Rathbun (1919b, 1935) from the Miocene of Florida, Dominican Republic, and Mexico. Judging by ecological requirements of living species, *Callinectes* would have been well

adapted to such an environment, but fossil evidence for its existence in the Paleocene remains indirect.

There are constant structural differences between the early fossil series and modern *Callinectes*. The palms of chelae of *C. jamaicensis* Withers, 1924 (Eocene), *C. alabamensis* Rathbun, 1935 (Oligocene), *C. declivis* Rathbun, 1919a (lower Miocene), and *C. reticulatus* Rathbun, 1919a (Oligocene-lower Miocene) are short and faceted more like *Callinectes* than other living genera of portunids, but they are relatively thinner than in living members of the genus. The fingers in these early forms have length-width proportions and tooth arrangements that resemble modern *C. sapidus*, but the tooth rows are relatively narrower proximally on propodal fingers and less inclined toward development of a molariform crushing surface. Of the four external facets on the palm, the upper mesial one in the fossil series is always inclined downward toward the inner surface in major chelae whereas in modern *Callinectes* species it is nearly horizontal in the major chela and noticeably inclined downward only in the minor one; moreover, the third or dorsolateral facet is relatively wider in living *Callinectes* species than in any of the early fossils. Compression and erosion may have altered relief but not uniform angle of inclination of facets in the fossils. Generally, fossils older than early-mid Miocene attributed to *Callinectes* have less powerful chelae than living species and these differences in structure seem significant enough to warrant generic separation of the two series when more material comes to light.

MODERN DISTRIBUTION

Confined almost exclusively to shallow, often brackish coastal waters as adults, the genus *Callinectes* is represented by six species distributed (Figures 24-27) around the Caribbean Sea and southward to southern Brazil: *C. marginatus, ornatus, danae, exasperatus, bocourti,* and *sapidus*. A seventh species, *C. maracaiboensis*, is localized in estuaries of Venezuela. One of these species, *C. marginatus*, bridges the Atlantic, ranging with *C. gladiator* and *C. latimanus* from Mauritania to Angola in West Africa. It also reaches the Cape Verde Islands. Only three species occur in the Gulf of Mexico, exclusive of the southeastern part off Florida: *C. rathbunae*, an isolated relative of *C. bocourti* in the western Gulf, *C. similis*, an essentially Carolinian form ranging northward along the coast, and *C. sapidus*, which ranges far beyond, occasionally to the Maritime Provinces of Canada. In the eastern Pacific, disregarding distant island occurrences, *C. arcuatus* is distributed from extreme southern California to Peru, sharing its range with *C. bellicosus* in the region of Baja California and with *C. toxotes* from there south.

If one relies on structure of male first gonopods alone for estimation of morphological similarity, the following zoogeographical associations emerge. The set of species with short first gonopods (*C. marginatus, gladiator, ornatus,* and *similis*) has separate eastern and western Atlantic components, and one member on both sides of the tropical Atlantic. The second set with longer first gonopods (*C. arcuatus, bellicosus, danae,* and *exasperatus*) occurs in the tropical western Atlantic and eastern Pacific. The third set with quite long first gonopods (*C. toxotes, bocourti, rathbunae, maracaiboensis, latimanus,* and *sapidus*) has representatives in all regions. Distributions of all species fit patterns accepted by Ekman (1953:30, ff.) as representative of many along the tropical-subtropical Atlantic and east Pacific coasts, but one, *C. sapidus*, has a latitudinal range that seems to exceed this pattern. In this species, development of a northern and southern form may be in progress.

The amphi-Atlantic distribution of *C. marginatus*, records of *C. exasperatus, marginatus, ornatus,* and *sapidus* from Bermuda, *C. arcuatus* from the Galápagos Islands, *C. toxotes* from Juan Fernández, as well as less removed northern marginal records for essentially southern species along the North American continent (*C. bocourti* in southern Florida and Mississippi; *C. marginatus* in North Carolina; *C. similis* in New Jersey; *C. sapidus* in Nova Scotia) all point to extensions of range by larval transport in currents (Verrill, 1908b; Garth, 1966). Investigators working with larval stages (reviewed in Williams, 1971) suggest that larvae and megalopae can move considerable distances; zoeae have been found off St. Johns River, Fla., at stations up to 160 km, and megalopae in the same area up to 128 km from shore. In Chesapeake Bay and Pamlico Sound, N.C., megalopae have been found 170 and 100 km respectively from presumed points of entry to the estuarine systems. Most of this off-and-onshore movement of larval stages appears to be a homeostatic developmental feature in the life

histories of the species. Among spiny lobsters, whose larvae are seemingly better fitted for temporary pelagic existence than crab larvae because of leaflike shape, up to 6 mo or greater duration of larval life occurs (Lewis, 1951; Austin, 1972). Phyllosomas of some spiny lobsters are rarely found beyond the latitudinal geographic limits of the coastal adult population. George and Main (1967) attributed this result to behavioral responses of the larvae, vertical migration, etc., within prevailing current systems which act to preserve integrity of distribution, but Austin (1972) held open the idea of long distance transport over considerable lengths of time. Some dispersal of larvae at the fringes of less pelagic *Callinectes* populations obviously occurs, but the wanderers are at a competitive disadvantage in establishing temporary range extensions. Nevertheless, larval dispersal of *Callinectes* coupled with movement of adults, judged to be minor except within an estuarine system (Fischler and Walburg, 1962; Tagatz, 1968), seems to assure genetic continuity over broad areas.

If one accepts the tenet that the center of evolution for a group contains the largest number of species, Neotropical Atlantic American shores seem to be the primary center in which the genus *Callinectes* developed and from which it radiated. Fossil evidence indicates that this radiation took place in the Tertiary, a period of time in which land-water relationships of that region diverged widely from their positional and areal extent today (Woodring, 1966, 1971). Olsson (1972) regarded the Miocene as the time when Panamanian molluscan biotas related to those of today evolved under conditions of general subsidence and when parts of present day Central America were reduced to an archipelago of large islands separated by straits between the Caribbean and east Pacific. Ekman (1953), Fell (1967), and others regarded the marine fauna that evolved in this region as an impoverished western outpost of the Tethyan fauna, related most closely to that of the eastern Atlantic and southern Europe. Though the tropical Atlantic and neighboring east Pacific regions both shared in the radiation of *Callinectes*, the conservatism of this offshoot contrasts remarkably with the far richer divergence of its parent stock. Stephenson (1962) considered the Indo-Pacific, with 175 living species, as the germinal center for the Portunidae. It seems reasonable to view *Callinectes* as a portunid group evolving at the geographic limits of the family, specializing in occupation of estuaries, and paralleling in many ways the heavy-bodied Indo-Pacific *Scylla serrata* (Stephenson, 1962).

If *Callinectes* evolved mainly in the Caribbean faunal province, the present distribution of species in essentially three isolated centers raises questions concerning dispersal. Separation of the east Pacific from the Caribbean by elevation of the Panamanian isthmus near the close of the Tertiary understandably isolated certain elements of the genus and may have promoted further radiation, but close relationship of species in the two areas is emphasized by an obvious geminate pair —*danae-arcuatus*—similar in a number of morphological features, which occurs today on east and west coasts of Middle and South America. Separation of the east and west Atlantic fragments of the genus is harder to resolve because not only does one species bridge this gap, but two species groups (short and long first gonopods) are represented on both sides of the ocean, seemingly specialized along the same general lines. Which is the ancestral stock? Were pelagic larvae the mechanism of transport, as Fell (1967) proposed for analogous but cold-tolerant echinoderms, perhaps aided by island stepping stones in the mid Atlantic? (Fell rejected continental drift as a plausible explanation for transport, an idea more acceptable today than it was in 1967, but involving a time span greater than concerned here [McKenzie, 1972].) Length of life of the larvae of most species of *Callinectes* under pelagic conditions remains unknown. West Africa is upstream from the Western Hemisphere in prevailing equatorial surface currents. It seems unlikely that the larvae could move counter to this current from a center in the west or survive the much longer (and today, colder) northern transit from the West Indies via the Gulf Stream beyond Bermuda to the Azores, Canaries, and finally to west Africa. So far as known, all *Callinectes* utilize estuaries during part of their lives. Populations on small islands may be nonbreeding, transitory implants, or unsuccessful breeders. Means and paths of long-distance transport, and effectiveness of transients in colonization, among these forms will remain unknown until more data are collected.

Finally, the clustering of species by numerical methods employed by Stephenson et al. (1968) does not reflect the three groups suggested by first gonopod types, but it does support classical interpretation setting *C. marginatus* and perhaps *C. gladiator* aside as the most peripheral morpholog-

ically. It suggests that the three west American species, *C. arcuatus, bellicosus,* and *toxotes* differ appreciably from each other and that they arose from eastern American ancestors. It also supports the idea that most of the postulated "central" species occur in the Atlantic and that "it is conceivable that the group originated from an eastern American ancestor." Beyond this the results are less compatible with conclusions reached here, but the analysis was done without including *C. similis* which may be a linking form that would have changed the interpretation.

SPECIES ACCOUNTS

In the species accounts that follow, the synonymies include only citations of works that primarily are concerned with descriptive, taxonomic, or zoogeographic information. The reason for this limitation is that commercially valuable species often have a voluminous literature. All inclusive synonymies for them become so unwieldy that the real purpose—taxonomic history of the species—becomes obscured. The descriptions also are limited because full descriptions are elsewhere in the literature.

Two features included in the descriptions need clarification. The term "metagastric area" is employed for the central trapezoidal area of the carapace in the sense Chace and Hobbs (1969) used it rather than the term "intramedial area" employed by others (cf. Rathbun, 1930; Williams, 1966). Strictly speaking, this region of the carapace includes the undifferentiated metagastric (over 90%) and at least part of the shortened urogastric (less than 10%) areas, but for all practical purposes the first term is sufficiently explicit. The number of anterolateral teeth in *Callinectes* is nine (Rathbun, 1930), but the first of the series is also known as the outer orbital tooth and the last as the lateral spine. This partition of the series is observed here. The first and last teeth are always named and the small teeth are numbered.

Abbreviations adopted for institutions loaning study material are: AHF, Allan Hancock Foundation, University of Southern California; AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Philadelphia; BMNH, British Museum (Natural History), London; MCZ, Museum of Comparative Zoology, Harvard; MNB, Museu Nacional, Rio de Janeiro; MNHNP, Museum National d'Histoire Naturelle, Paris; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden; SADZ-B, Secretaria da Agricultura, Departamento Zoologia, São Paulo; UNC-IMS, University of North Carolina, Institute of Marine Sciences, Morehead City; USNM, National Museum of Natural History, Washington, D.C.; YPM, Peabody Museum of Natural History, Yale University, New Haven, Conn.

Supplementary literature records are occurrences not represented by specimens studied, but accepted on basis of supporting data.

GENUS *CALLINECTES* STIMPSON, 1860

Callinectes Stimpson, 1860, p. 220 [92].- Rathbun, 1896, p. 349 (revision).- 1921, p. 394 (review of African species).- 1930, p. 98 (review of Western Hemisphere species).- not Chen, 1933, p. 95 (=*Portunus*?).- Monod, 1956, p. 204 (review of African species).- Garth and Stephenson, 1966, p. 42 (review of eastern Pacific species).

Description.—Portunid crabs lacking an internal spine on carpus of chelipeds. Abdomen of males broad proximally, narrow distally, roughly T-shaped; first segment broad, almost hidden; second segment broad, slightly overlapping coxae of fifth pereopods at each side; third-fifth segments fused and tapering sinuously from broad third to distally narrow fifth; sixth segment elongate and narrow; telson ovate with acute tip. Abdomen of females exhibiting two forms: immature females with abdomen triangular from fourth segment to tip of telson, segments fused; mature females with abdomen broadly ovate (excluding telson), segments freely articulated; first segment almost hidden; second and third segments slightly overlapping coxae of fifth pereopods at each side; fifth and sixth segments with greatest sagittal length; sixth segment narrowing distally in irregular broad arc to articulate with triangular telson. Abdomen and telson of both sexes reaching anteriorly beyond suture between thoracic sternites IV and V.

Type species.—*Callinectes sapidus* Rathbun, 1896, by designation of International Commission of Zoological Nomenclature (1964:336).

Gender.—Masculine.

Number of species.—Fourteen, which may be distinguished by the following keys.

KEY TO SPECIES OF *CALLINECTES* (EXCLUDING JUVENILES)

Figures 3-17

1. Front with two prominent, broad based, triangular teeth between inner orbitals; each with or without rudimentary submesial tooth on mesial slope (Atlantic; Western Hemisphere, introduced in Europe) ..... *sapidus.*
1′. Front with four teeth between inner orbitals, or two prominent lobulate or narrowly triangular teeth separated by a nearly plane space often bearing a pair of rudimentary submesial teeth 2
2. Submesial pair of frontal teeth well developed and more than half as long as lateral pair (measuring from base of lateral notch between teeth) 3
2′. Frontal teeth decidedly unequal in size, submesial pair no more than half as long as lateral pair (measuring from base of lateral notch between teeth), or vestigial 8
3. Four frontal teeth reaching nearly common level 4
3′. Submesial frontal teeth definitely falling short of lateral pair 7
4. Four frontal teeth lobulate, not triangular (Pacific; Baja California–Juan Fernández) *toxotes.*
4′. One or both pairs of frontal teeth triangular 5
5. Four frontal teeth with rather rounded tips, lateral pair more broadly triangular than submesial pair and with mesial side having more oblique slope than lateral side .. 6
5′. Four frontal teeth acute, lateral pair usually broader than submesial pair (Atlantic; Mexican Gulf coast) ..... *rathbunae.*
6. Anterolateral teeth trending forward, their anterior margins shorter than posterior; vestiges of reddish color usually persisting in preserved specimens (except long-preserved ones); distal border of sixth abdominal segment in mature females broadly triangular (Atlantic; Caribbean-South America) ..... *bocourti.*
6′. Anterolateral teeth directed outward, their tips acuminate and margins shouldered at least in anterior portion of row; vestiges of greenish color usually persisting in preserved specimens (except in long-preserved ones); distal border of sixth abdominal segment in mature females semiellipsoid (Atlantic; Venezuelan estuaries) ... *maracaiboensis.*
7. Granules on ridges and crests of chelae coarse and well separated (Atlantic; Caribbean-South America) ..... *exasperatus.*
7′. Granules on ridges and crests of chelae moderate to fine and closely crowded, often worn smooth in adults (Atlantic; West Africa) ..... *latimanus.*
8. Carapace remarkably smooth, lines of granules visible but barely perceptible to touch (except epibranchial line variably prominent) 9
8′. Carapace not so smooth, scattered granules and lines of granules quite evident to sight and touch 10
9. Submesial pair of frontal teeth vestigial (Pacific; Baja California and Golfo de California) *bellicosus.*
9′. Submesial pair of frontal teeth small but definitely formed (Atlantic; United States-Gulf of Mexico) ..... *similis.*
10. Carapace coarsely granulated; all anterolateral teeth except first two curved forward, without shoulders (Atlantic; Bermuda-Florida–South America-West Africa) .... *marginatus.*
10′. Carapace finely granulated; only last or last two anterolateral teeth curved forward, remainder with shoulders 11
11. Submesial pair of frontal teeth absent or vestigial (Atlantic; Bermuda-North America-South America) ..... *ornatus.*
11′. Submesial pair of frontal teeth never vestigial, but no more than half length of lateral pair 12
12. Lateral spine almost always less than three times length of preceding anterolateral tooth; tips of anterolateral teeth forming a decided arc; males with distal portion of first gonopods almost straight 13

12′. Lateral spine almost always three or more times length of preceding anterolateral tooth; at least second to fifth anterolateral teeth with tips in a nearly straight line; males with distal portion of first gonopods S-curved (Atlantic; West Africa) ..... *gladiator.*
13. First gonopods of mature males with subterminal dorsal setae never more than four in number, often inconspicuous or missing (Atlantic; Caribbean-South America) ..... *danae.*
13′. First gonopods of mature males with subterminal dorsal row of setae numbering more than four (Pacific; Southern California-Peru; Galápagos Islands) ..... *arcuatus.*

KEY TO MATURE OR NEARLY MATURE MALE *CALLINECTES* BASED PRIMARILY ON FIRST GONOPODS

Figures 18-21

1. Tips of gonopods falling well short of suture between thoracic sternite VI and mesially expanded sternite VII 2
1′. Gonopods reaching to, almost to, or beyond suture between thoracic sternite VI and mesially expanded sternite VII 5
2. Gonopods well separated from each other, never touching or crossed 3
2′. Gonopods overlapping each other, often crossed 4
3. Gonopods slender distally, nearly straight, tips bent slightly mesad (Atlantic; United States-Gulf of Mexico) ..... *similis.*
3′. Gonopods fairly stout distally, angled toward midline, then abruptly bent forward in a short slender terminal extension (Atlantic; Bermuda-Florida-South America-West Africa) ..... *marginatus.*
4. Tips of gonopods lanceolate, continuing in line with shaft, portion proximal to tip armed with short backward pointing spines quite visible at low magnification (Atlantic; Bermuda-North America-South America) ..... *ornatus.*
4′. Tips of gonopods not lanceolate, curved mesad, spines on S-curved shank exceedingly small at low magnification (Atlantic; West Africa) ..... *gladiator.*
5. Tips of gonopods curved abruptly mesad (Atlantic; Caribbean–South America) .... *exasperatus.*
5′. Tips of gonopods not curved abruptly mesad 6
6. Slender portion of gonopods almost straight, minutely spined (under magnification), tips almost always bent ventrolaterally, never extending beyond abdominal locking tubercle on thoracic sternite V 7
6′. Slender portion of gonopods definitely curved or sinuous, variously spined, tips never bent ventrolaterally 8
7. Gonopods with subterminal dorsal setae never more than four in number, often inconspicuous or missing (Atlantic; Caribbean–South America) ..... *danae.*
7′. Gonopods with subterminal dorsal row of setae numbering more than four (Pacific; Southern California-Peru; Galápagos Islands) ..... *arcuatus.*
8. Tips of gonopods reaching well beyond abdominal locking tubercle on thoracic sternite V 9
8′. Tips of gonopods not reaching beyond abdominal locking tubercle on thoracic sternite V (Pacific; Baja California and Golfo de California) ..... *bellicosus*
9. Slender portion of gonopods with spinules small under magnification and most dense near middle, absent near tip (Pacific; Baja California-Juan Fernández) ..... *toxotes.*
9′. Slender portion of gonopods with spinules readily visible at low magnification and distributed to tip 10
10. Gonopodal spines arranged in a broad dorsolateral band 11
10′. Gonopodal spines arranged in a single, rather uneven dorsolateral row (a few tiny spines lying outside row) (Atlantic; Western Hemisphere, introduced in Europe) ..... *sapidus.*
11. Tips of all frontal teeth reaching same level 12
11′. Submesial pair of frontal teeth definitely shorter than lateral pair (Atlantic; West Africa) *latimanus.*

12. Four frontal teeth with rather rounded tips, lateral pair more broadly triangular and with mesial side having more oblique slope than lateral side 13
12′. Four frontal teeth acute, lateral pair usually broader than submesial pair (Atlantic; Mexican Gulf coast) ..... *rathbunae.*
13. Anterolateral teeth trending forward, their anterior margins shorter than posterior; vestiges of reddish color usually persisting in preserved specimens (except long-preserved ones); (Atlantic; Caribbean-South America) ..... *bocourti.*
13′. Anterolateral teeth directed outward their tips acuminate and margins shouldered at least in anterior portion of row; vestiges of greenish color usually persisting in preserved specimens (except in long-preserved ones); (Atlantic; Venezuelan estuaries) ..... *maracaiboensis.*

CALLINECTES MARGINATUS (A. MILNE EDWARDS)

Figures 3, 18a, 20a, 22b, 27

Neptunus marginatus A. Milne Edwards, 1861, p. 318, pl. 30, fig. 2 (syntypes: 3 ♀ dry, MNHNP 895-1S, 895-2S, 896, Gabon).

Callinectes larvatus Ordway, 1863, p. 573 [8] (syntypes: 1 ♂, MCZ 5147, Tortugas, Fla., USA; 3 ♂, 1 ♀, MCZ No. 5151, Key West, Fla., USA; 3 ♂ MCZ 5152, Bahamas; 1 ♂, 1 juv ♀ [not ♂], MCZ 5155, Jeremie, Haiti).- Smith, 1869, p. 9.- A. Milne Edwards, 1879, p. 225 (var. of *C. diacanthus*).- Rathbun, 1896, p. 358, pl. 18, pl. 24, fig. 5; pl. 25, fig. 4; pl. 26, fig. 4; pl. 27, fig. 4.- Rankin, 1898, p. 232.- Young, 1900, p. 188 (var. of *C. diacanthus*).- Doflein, 1904, p. 99.

Neptunus diacanthus.- Brocchi, 1875, pl. 16, fig. 76 [?].- de Man, 1883, p. 150.- Pfeffer, 1890, p. 5, pl. 1, figs. 5, 6.

Callinectes africanus A. Milne Edwards, 1879, p. 229 (var. of *C. diacanthus*) (syntypes: MNHNP, Cape Verde Islands, not found in 1968).- A. Milne Edwards and Bouvier, 1900, p. 71 (var. of *C. diacanthus*) (not pl. 4, fig. 5 = *C. sapidus*).

Callinectes larvatus var. *africanus?* Benedict, 1893, p. 537.

Neptunus (Callinectes) diacanthus.- Ortmann, 1894, p. 77 (part; specimen b, Cuba).

Callinectes marginatus.- Rathbun, 1897, p. 149.- 1900a, p. 291.- 1900b, p. 142.- 1901, p. 48.- 1921, p. 395, text-fig. 2, pl. 19, fig. 1; pl. 20, fig. 1.- 1930, p. 123, figs. 15e, 16d, 17d, 18c, pl. 53.- 1933, p. 49.- 1936, p. 383.- de Man, 1900, p. 41, pl. 1, fig. 5 (juv ♀, not ♂).- Nobili, 1906, p. 305.- Gruvel, 1912, p. 3, 6, pl. 2, fig. 1.- Balss, 1921, p. 58.- Odhner, 1923, p. 21.- Boone, 1927, p. 32.- Contreras, 1930, p. 235, fig. 6.- Vilela, 1949, p. 59.- Capart, 1951, p. 134, fig. 48.- Chace, 1956, p. 154.- Chace and Hobbs, 1969, p. 131, fig. 37d.- Monod, 1956, p. 208, figs. 238, 239.- Rossignol, 1957, p. 82.- Guinot and Ribeiro, 1962, p. 48.- Forest and Guinot, 1966, p. 65.- Taissoun, 1973, p. 39, figs. 4A, 5B, photo 7.

Callinectes diacanthus.- Young, 1900, p. 186 (part).

Callinectes marginatus var. *larvatus*.- Verrill, 1908a, p. 368, text-fig. 22b, pl. 18, fig. 1.

Description.—Carapace (Figure 3) bearing four frontal teeth, submesial pair no more than half length of lateral pair. Central trapezoidal (metagastric) area short, anterior width about 2.4 times length, posterior width about 1.5 times length. Anterolateral margins arched slightly; anterolateral teeth exclusive of outer orbital and lateral spine without shoulders, usually trending forward and anterior margins of all except first two concave, last two teeth spiniform. Lateral spine moderately long and slender. Surface coarsely granulate anterior to prominent epibranchial line and over mesobranchial regions, more finely and closely granulate on proto- and mesogastric areas, prominent branchial lobes, and especially on cardiac lobes; posterior and posterolateral margins smooth.

Chelipeds with smoothly granulate prominent ridges on propodi and reduced ones on carpi; fingers compressed but broadened dorsoventrally producing a pointed spatulate shape; major chela with usual enlarged proximal tooth on dactyl opposing propodal molariform complex, propodus often with decurved lower margin.

Male abdomen and telson narrow, reaching slightly beyond suture between sternites IV and V; telson about 1.8 times longer than wide; sixth

TABLE 1.—Mean measurements ($\bar{x}$) in mm, with standard deviations (s) and sample sizes (N), of selected characters for adult male *Callinectes*. Refer to Figures 1 and 2 for illustration of measurements.

Measurements	*arcuatus*			*bellicosus*			*bocourti*			*danae*			*exasperatus*			*gladiator*			*latimanus*		
	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N
Length	42.3 ± 7.4		74	58.5 ± 17.0		28	55.0 ± 9.0		46	46.5 ± 5.8		84	52.6 ± 7.0		54	35.0 ± 6.3		23	53.9 ± 10.4		27
Width																					
incl. lat. spines	94.0	18.7	75	118.3	33.7	28	109.3	20.0	45	108.7	14.7	84	101.6	14.0	54	87.0	15.4	23	112.8	23.2	26
base lat. spines	74.5	13.9	75	104.5	31.0	28	94.5	15.7	45	83.4	10.7	84	89.2	12.2	54	65.3	11.7	23	96.3	22.6	27
Max. height	24.6	4.5	74	33.4	9.5	25	31.9	5.2	45	25.8	3.4	84	31.6	4.4	54	20.8	4.2	23	32.1	12.0	27
Metagastric																					
ant. width	17.18	3.08	74	24.59	7.22	25	19.73	3.48	46	18.91	2.48	84	21.40	2.96	54	14.4	2.70	23	20.10	4.28	27
length	7.08	1.38	74	8.97	2.85	25	9.95	1.74	46	7.71	1.12	84	9.03	1.39	54	5.52	1.10	23	9.74	2.12	27
post. width	9.41	1.72	74	14.16	3.96	26	10.42	1.85	46	10.92	1.50	84	11.25	1.66	54	8.34	1.65	23	10.35	2.13	27
Telson																					
length	5.12	0.89	66	6.97	1.88	27	9.82	1.84	44	5.51	0.83	82	6.63	1.04	52	4.39	0.72	23	9.72	1.88	26
width	3.37	0.51	67	4.57	0.92	27	4.86	0.61	44	3.73	0.62	81	4.40	0.82	52	2.73	0.41	23	5.13	0.83	26

Measurements	*maracaiboensis*			*marginatus*			*ornatus*			*rathbunae*			*sapidus*			*similis*			*toxotes*		
	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N
Length	57.8 ± 7.8		11	42.6 ± 6.4		82	41.6 ± 7.8		81	52.8 ± 5.2		5	63.2 ± 13.9		65	43.3 ± 5.8		26	71.3 ± 11.6		24
Width																					
incl. lat. spines	113.7	16.8	11	93.8	14.7	82	91.2	16.4	80	112.8	13.4	5	142.8	35.2	65	97.6	13.1	26	153.1	27.5	24
base lat. spines	97.8	12.7	11	77.5	12.5	82	72.5	14.0	81	92.2	9.4	5	115.1	26.3	65	75.7	10.4	26	125.9	21.9	24
Max. height	33.1	4.2	11	24.6	3.8	81	23.6	4.8	81	30.4	3.4	5	36.4	8.5	61	23.5	3.2	26	39.8	6.3	24
Metagastric																					
ant. width	21.21	2.64	8	17.05	2.74	82	18.75	3.95	81	18.92	2.73	5	23.60	5.32	65	18.64	2.94	26	25.53	4.25	24
length	8.81	3.66	9	7.11	1.22	82	6.57	1.30	81	9.30	1.09	5	10.60	2.59	65	6.81	1.04	26	12.14	2.07	24
post. width	8.15	4.04	8	10.60	1.49	82	11.49	2.07	81	9.80	1.54	5	12.85	2.89	65	11.09	1.55	26	12.11	2.12	24
Telson																					
length	14.08	1.23	11	5.74	1.18	79	4.99	1.02	78	9.56	0.95	5	9.95	2.42	65	5.25	0.75	26	10.91	1.71	23
width	6.07	0.44	11	3.19	0.59	79	3.04	0.54	78	4.74	0.44	5	5.66	1.23	65	3.65	0.37	26	5.93	0.68	23

TABLE 2.—Mean measurements ($\bar{x}$) in mm, with standard deviations (s) and sample sizes (N), of selected charaters for adult female *Callinectes*. Refer to Figures 1 and 2 for illustration of measurements.

Measurements	*arcuatus*			*bellicosus*			*bocourti*			*danae*			*exasperatus*			*gladiator*			*latimanus*		
	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N
Length	36.5 ±	8.1	30	56.4 ±	6.6	16	51.6 ±	6.7	30	40.8 ±	3.9	52	49.5 ±	5.0	32	29.9 ±	5.7	45	53.5 ±	4.9	19
Width																					
incl. lat. spines	78.9	16.8	30	110.8	14.2	16	106.2	14.0	31	92.9	9.0	52	97.1	10.6	32	73.3	12.6	45	117.2	10.5	18
base lat. spines	62.9	14.0	30	97.0	12.1	16	88.1	11.3	31	71.7	7.1	51	82.8	8.6	32	54.8	10.1	45	94.5	9.0	19
Max. height	22.0	5.2	29	33.6	4.4	16	31.0	4.2	30	23.7	2.3	52	30.8	3.4	31	18.7	3.5	45	32.3	3.1	18
Metagastric																					
ant. width	16.02	3.34	29	24.70	2.85	15	19.76	2.90	30	17.57	1.78	52	21.90	2.18	32	13.03	2.11	44	20.94	3.99	19
length	6.34	1.46	29	9.43	0.96	15	9.72	1.27	30	7.00	0.81	52	8.85	1.01	32	4.93	1.10	44	10.05	1.06	19
post. width	9.14	1.98	29	14.38	1.30	15	10.90	1.75	30	10.47	1.13	52	11.85	1.30	32	7.65	1.21	44	11.67	1.10	19
Telson																					
length	4.19	1.01	30	6.92	0.97	16	7.76	1.19	29	4.94	0.56	50	6.25	0.79	31	3.65	0.94	45	8.03	0.97	19
width	4.39	0.95	30	7.02	0.75	16	6.53	0.83	29	5.04	0.50	50	6.54	0.80	31	3.77	0.92	45	7.12	0.63	19
Abd. seg. length																					
5th	7.04	1.75	30	11.84	1.69	16	10.70	1.56	30	8.03	1.37	51	10.63	1.28	32	6.14	1.59	45	11.09	1.18	19
6th	7.38	1.86	29	11.76	1.49	16	11.23	2.15	29	8.16	0.96	48	9.89	1.10	30	5.68	1.42	45	13.89	7.36	19

Measurements	*maracaiboensis*		*marginatus*			*ornatus*			*rathbunae*			*sapidus*			*similis*			*toxotes*		
	$\bar{x}$	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N	$\bar{x}$	s	N
Length	53.3	3	38.7 ±	3.8	42	36.5 ±	8.4	43	57.0 ±	7.4	5	54.7 ±	12.7	69	35.4 ±	5.2	39	66.9 ±	3.9	13
Width																				
incl. lat. spines	114.3	3	83.5	8.5	42	77.7	12.5	43	126.6	12.6	5	131.0	34.3	69	76.9	11.8	39	148.9	11.5	13
base lat. spines	91.7	3	68.9	6.9	42	29.5	4.8	43	101.6	12.0	5	99.4	24.1	68	60.9	9.0	39	117.9	7.6	13
Max. height	31.3	3	23.3	2.5	42	20.5	4.3	42	34.0	5.0	5	31.8	7.9	64	19.8	2.9	39	39.4	2.6	13
Metagastric																				
ant. width	20.40	3	16.23	2.46	41	16.86	2.96	42	22.88	3.36	5	21.66	4.97	69	15.77	3.09	39	25.80	1.92	13
length	9.53	3	6.69	0.80	41	5.88	1.04	42	10.12	1.34	5	9.38	2.39	69	5.70	0.89	39	12.00	0.69	13
post. width	11.23	3	10.24	1.33	41	10.46	1.97	42	12.64	2.46	5	12.13	2.67	69	9.67	1.41	39	13.10	1.03	13
Telson																				
length	8.20	3	5.11	0.56	40	4.24	0.86	43	8.24	1.51	5	7.94	1.91	67	4.08	0.70	39	9.48	0.64	13
width	7.10	3	4.91	0.53	40	4.27	0.81	43	7.36	1.06	5	7.03	1.52	67	4.48	0.55	39	8.16	0.76	13
Abd. seg. length																				
5th	11.27	3	7.93	0.93	41	6.70	1.46	43	12.52	1.86	5	12.09	2.99	66	7.10	1.11	39	13.88	1.32	13
6th	11.57	3	8.06	0.90	39	7.04	2.93	41	16.86	8.79	5	11.96	3.14	65	7.30	1.18	38	14.24	3.01	13

segment nearly parallel sided but somewhat broadened proximally. Mature female abdomen and telson reaching same level as in male, length slightly exceeding width (1.05 times); sixth segment longer than fifth. First gonopods of male (Figures 18a, 20a) short, reaching about mid-length of sternite VII, approximating each other or occasionally overlapping at level of sharp distal curve, distal portion abruptly curved laterad, tapered to a rather sharp point, twisted one-fourth turn on axis and, except for membranous spout-like tip, armed with minute scattered retrogressive spinules tending to arrangement in rows, a few spinules proximal to flexure. Gonopores of female (Figure 22b) ovate with apex on long axis directed anteromesad, aperture of each with margin irregularly rounded and sinuous except on mesial side where it slopes from surface laterad under superior anterior border.

Size of carapace in mm.—Largest male: length 67, width at base of lateral spines 118, including lateral spines 142. Largest female: length 49, width at base of lateral spines 82, including lateral spines 95. Mature size of females varies considerably, the smallest examined having a carapace length of 33 and width including lateral spines of 70. Summary of selected measurements is given in Tables 1 and 2.

Color.—Carapace brown with areas of bluish black. Chelae brown above; fingers dark on external face except for tips and proximal portion, internal face dark in distal two-thirds; dark color of fingers retained in preservation (in part from Rathbun, 1930, and pers. commun. from Charles A. Johnson). Milne Edwards and Bouvier (1900) gave essentially the same impression, characterizing the entire carapace, abdomen, external face of chelipeds, posterior legs, some areas of the walking legs with their marginal hairs as greenish brown and other parts of the appendages as a beautiful blue, but there is some confusion here because the colored plate accompanying this description (Plate 4, Figure 5) represents *C. sapidus*. Rossignol (1957) described the carapace as marbled, and recently preserved material in alcohol sometimes does give an impression of mottled gray and white on the carapace.

Variation.—The carapace in *C. marginatus* shows a number of individual variations. The small anterolateral teeth generally trend forward, but there is enough individual departure from this pattern to cause confusion. Teeth in the mesial part of the row trend forward more than those in the lateral part, the first three often being rounded while the last four are pointed. Small anterolateral teeth on syntype females in MNHNP do not definitely trend forward, and those on the syntype of *C. larvatus* (MCZ 5155) are well separated, with apices directed outward rather than hooked forward. There are differences, too, in width of the anterolateral teeth, a suggestion of narrower teeth in Brazil than in Florida, and broad teeth on some African material. Occasionally there is some iridescence along the anterolateral border, and often hairiness along the lower anterolateral border.

The inner orbital fissures are usually tightly closed, sometimes with a slight notch on the orbital border, but open in some African and Dutch West Indies (Aruba) material.

The anterolateral slopes have an arching concavity proximal to the bases of the anterolateral teeth and extending transversely behind the orbitofrontal region that is more pronounced than in other species of the genus. This is especially evident in mature females. The abdomen of immature males is flush with the sternum and relatively wider than in adults in which it is somewhat recessed. Among mature males, calcification is weak in the articulation between the fifth and sixth abdominal segments allowing definite flexure in this joint, but transverse ridges ("stops") on external exposed edges of the joint prevent doubling backward. The calcification pattern is well demonstrated in two mature males in USNM 4172 from Dominican Republic. Abdominal segment 6 is constricted at mid-length in some males. The abdomen of adult females resembles that of *C. ornatus*.

Sexual differences include a more tumid appearing body among females than males, an effect resulting partly from less produced lateral spines, as well as granulations on the carapace that are relatively more prominent than on males. Granules on the carapace sometimes are very coarse in front of the epibranchial line, but seldom as coarse behind as in front of this line. Inconspicuous spination on the male first gonopods in specimens from the Canal Zone of Panama, Honduras, Colombia, and Venezuela is not so strong nor dense as that in males from Florida where there is a suggestion that the scattered spines are in rows proximal to the distal bend; spination

seems entirely lacking in some Brazilian material.

This is the species that should be named "latimanus" because broad, spatulate, often strongly asymmetrical chelae occur on both juveniles and adults. The chelipeds often seem heavy for the size of the animal bearing them, but pronounced asymmetry is not universally present. Some individuals have both chelae basically alike except for size, and in almost all except juveniles the ventral side of the propodus (especially the major) is decurved in a wide sweep giving emphasis to the "spatulate" character. The proximal tooth on the dactyl of the major chela may be moderate but is often large in size and worn as shown in Figure 3a. Some juveniles with worn chelae have a gape between fingers of the minor as well as major chela along with development of a strong proximal tooth on the dactyls. Although similarity in chelae may indicate regeneration, there is no evidence that replacement has occurred.

Habitat.—Meager data recorded with specimens suggests that this species lives in a variety of shallow littoral environments probably seldom exceeding 15 m (rarely to 25 m [?]) and usually in much shallower water from intertidal pools to 3 m deep. Most specimens have been collected by hand, seine, dip net, etc., from sand and mud flats, algae and grass flats, sandy beaches, rocky pools, eroded coral bases, oyster bars, shallows at edge of mangroves, and at the surface under lights at night. A number of authors (Milne Edwards and Bouvier, 1900; Monod, 1956; Rossignol, 1957; Forest and Guinot, 1966; Coêlho, 1967a, b, 1970) have noted that *C. marginatus* is a coastal species limited to depths of a few meters, often in brackish water, but rather rare and never as abundant as other species of *Callinectes*. Capart (1951) found it on shallow mud bottoms in salinities varying from 7.43-14.85‰ at the surface to 19.29-32.56‰ in 5-m depths and in a bottom temperature range of 22.5° to 27.42°C; he never found it in the ocean. Buchanan (1958) similarly found it in 5.5-14-m depths in a temperature range of 27° to 30°C off Accra, Ghana, in what he termed the inshore fine sand community. Chace (1956) recorded it in 27.5°C water off Los Roques, Venezuela.

Spawning.—Both the museum material studied and records in literature yield only fragmentary evidence on spawning. Ovigerous females are recorded from December to July in various parts of the geographic range on both sides of the Atlantic. Specifically the records are: Congo and St. Thomas, December; St. Thomas, January; Grenadines and Cuba, March; Haiti, April; Jamaica and Senegal, May; Colombia, Curaçao and São Tomé (Forest and Guinot, 1966), June; Florida and Puerto Rico, July.

Distribution.—Off southern Florida through Caribbean Sea to south central Brazil off Estado de São Paulo; Bermuda and Cape Verde Islands; Senegal to central Angola (Figure 27). A recent record from North Carolina is regarded as a temporary range extension.

Economic importance.—Gravel (1912), describing fisheries for *C. latimanus* along the Gulf of Guinea, noted that *C. marginatus* is also caught all along the coast from Senegal to the Congo under a variety of local names.

Remarks.—The populations on each side of the Atlantic seem indistinguishable by means of external morphological characters. Different names applied to the populations on each side reflect the discontinuity of early collections, Verrill (1908a) for instance considering *larvatus* the American and *africanus* the African variety, but with the progress of exploration and inventory it is evident that the whole is a genetic continuum with minor local variations already pointed out. Most modern workers (Capart, 1951; Monod, 1956) accept this idea although deploring the difficulty in identifying juveniles.

Verrill (1908b) early recognized the significance of larval transport in oceanic currents, applying it to populations of *C. marginatus* in Bermuda that have their origin in the West Indies. It is tempting to make the generalization that this species in its moderate size, short, simply ornamented male first gonopods, and amphi-Atlantic pattern of geographic distribution possibly represents an unspecialized and primitive member of the genus, but such ideas are qualified by the specialization of chelae seemingly well adapted by their dorsoventrally broadened but rather thin fingers for reaching into crevices, perhaps into mollusk shells after they are cracked. In short, generalized structure is hard to assess.

Some specimens show evidence of massive fouling by the barnacle *Chelonibia*. A male (dry) from Brazil (BMNH 48.86) measuring 89 mm between

tips of lateral spines bears the basal disc of a barnacle measuring 24.9 × 26.2 mm, or an oval area covering all of the metagastric and a portion of the right branchial lobe forward to the base of the frontal margin and edge of the right orbit. A second and still intact barnacle covers all of the left mesobranchial region (11.7 × 13.0 mm).

Material.—Total. 242 lots, 615 specimens.

Specimens listed in Rathbun (1930) from USNM (31091, 4172, 24445, 24446, 24447, 24448, 24449, 24450, 24454, 43905, 62684, 54255 not found; 32514 = *C. ornatus*, 33103 = *C. similis*, 61364 = *C. danae*) and MCZ.

USNM. 99 lots, 282 specimens, including the following not cited above:

UNITED STATES

Florida: 80624, Lake Worth, 1945, 1 ♂, A. H. Verrill. 113458, Pigeon Key, Monroe Co., 7 Aug. 1965, 1 ♂, R. B. Manning. 123063, Bahia Honda Key, Monroe Co., 14 June 1964, 2 ♂, 2 juv, Foster and Kaill, No. 64-11-I. 71635, Key West, 1934, 1 ♂, H. H. Darby. 76972, Key West, no date, 5 ♂, 1 ♀ (ov), C. J. Maynard. 123075, Key West, no date, 3 ♂, 2 ♀, U.S. Bur. Fish. The following from Dry Tortugas—62156, 25 July 1928, (juv) 2 ♀, A. S. Pearse. 76968, Fort Jefferson, Aug. 1930, 1 ♂, W. L. Schmitt. 62155, Loggerhead Key, 6 Aug. 1928, 2 ♂ (juv), A. S. Pearse. 76967 and 76970, Long Key, 25 June 1931, 1 ♂, 5 juv, W. L. Schmitt. 76969, Long Key-Bush Key, 18 June 1932, 1 ♂, W. L. Schmitt. 71636, Bush Key, 4 Aug. 1934, 1 ♀, H. H. Darby. 71655, Sarasota Bay, summer 1930, 1 juv, W. W. Wallis.

BAHAMAS

101130, Bimini Bay, 27 Nov. 1951, 1 ♂ (juv), F. Frieders.

CUBA

99977, E Xanadú, Hicacos Pen., Matanzas Prov., 24-27 Jan. 1957, 1 carapace, W. L. Schmitt.

JAMAICA

123060, N shore, 18°24.5′N, 77°07′W, 20 May 1965, 1 ♀ (ov), *Oregon* Stn. 5405. 123062, Kingston Harbor, 17 May 1965, 1 ♀, B. B. Collette.

HAITI

65859, Ile a Vache, 29 Apr. 1930, 1 ♀ (ov), W. M. Parish. 81481, I. opposite Bayeaux, 23 June 1941, 1 ♂, H. H. Bartlett.

DOMINICAN REPUBLIC

62828, near Montecristi, winter 1928-29, 1 chela, H. W. Kreiger.

PUERTO RICO

73282, off Fort San Gerónimo, San Juan, 30 Apr. 1937, 3 ♂, W. L. Schmitt. 73285, near Fort San Gerónimo, W end San Juan I., 27 Mar. 1937, 1 ♀, W. L. Schmitt.

VIRGIN ISLANDS

St. Croix: 72351 and 72359, Salt River Bay, 1935-36, 2 ♂, H. A. Beatty. 73284, Christiansted, 9 Apr. 1937, 1 ♂, W. L. Schmitt. 76964 and 76965, Envy Bay, no date, 1 ♂, 2 ♀, H. A. Beatty. Prickly Pear I. 123070, Vixen Pt., Gorda Sound, 15 Apr. 1956, 1 ♀ (juv), Nicholson, Schmitt, and Chace.

BARBUDA

123069, near Oyster Pond Landing, 6 Apr. 1956, 1 ♂, Schmitt, Chace, Nicholson, and Jackson.

ANTIGUA

123068, Tank Bay, English Harbor, 3 Apr. 1956, 3 ♂, Schmitt, Chace, Nicholson, and Jackson.

GUADELOUPE

123067, between Monroux and Rat Is., Pointe à Pitre, 30-31 Mar. 1956, 21 ♂, 5 ♀, 13 juv, Chace and Nicholson.

ST. LUCIA

123066, shore of bay outside Marigot Lagoon, 21 Mar. 1956, 1 ♂, Chace, Nicholson, and crew.

GRENADINES

123064, Tyrrell Bay, Carriacou I., 15 Mar. 1956, 3 ♀ (ov), Schmitt and Nicholson. 123065, Tyrrell Bay, Carriacou I., 16 Mar. 1956, 1 ♀, D. V. Nicholson.

MEXICO

Quintana Roo: 123072, Cozumel I., near lighthouse at Punta Molas, 9 Apr. 1960, 5 ♂, Rehder and Bousfield. 123071, Bahía del Espíritu Santo, north shore near Lawrence Pt., 6 Apr. 1960, 1 ♂, Rehder, Daiber, and Haynes. 123073, Pt. Santa María [20°19′N, 86°59′W], 22 Apr. 1960, 1 ♂, Schmitt and Rehder.

HONDURAS

78107, Utila I., Sept. 1938, 1 ♂, L. Mouquin.

COLOMBIA

123061, Isla de San Andrés, 5 June 1964, 1 ♀ (ov), B. A. Rohr.

PANAMA

61427, Margarita I. [09°23′N, 79°53′W], June 1924, 1 ♀, E. Deichmann.

BRAZIL

Bahia: 123074, Plataforma, 1875-77, 1 ♂, 1 ♀ (ov), Hartt Exped. Rio de Janeiro: 123076, São Francisco, 25 Aug. 1925, 1 ♂, W. L. Schmitt.

ZAIRE

54255, Banana, mouth of Congo River, July-Aug. 1915, 1 ♀, H. Lang.

AHF. 7 lots, 12 specimens.

UNITED STATES

Florida: Key Largo S Gordons Landing at Rock Harbor, 19 Sept. 1950, 2 ♂, 1 ♀, Stn. LM52. Hawk Channel, Plantation Key, 3 mi S Tavernier bridge, 25 May 1949, 1 ♀, A126-49, Stn. LM20-49. Hawk Channel off Lower Matecumbe Key, 9 June 1949, 2 ♂, 1 ♀, A140-49, Stn. LM34-49. Hawk Channel, Lower Matecumbe Key, 23 Sept. 1950, 2 ♀, Stn. LM57. Long Key, Florida Bay, 10 June 1949, A141-49, Stn. LM35-49.

TOBAGO

Bucco Bay, 11°10′42″N, 60°48′07″W, 20 Apr. 1939, 1 ♂, *Velero III*, Stn. A40-39.

TRINIDAD

Port of Spain, 10°38′12″N, 61°32′08″W, 18 Apr. 1939, 1 ♀, *Velero III*, Stn. A37-39.

AMNH. 30 lots, 81 specimens.

UNITED STATES

Florida: Lake Worth, July and Aug. 1945, 1 ♂ (juv), W. G. Van Name. 9789, Lake Worth, June 1945, 1 ♂, A. H. Verrill. 2290, Key Largo, no date, 1 ♂, C. W. Beebe.

BAHAMAS

11222, North Bimini, June 1939, 7 ♂, W. Beebe Bermuda Exped. 11288 and 11289, Bimini, 5 Sept. 1947, 2 ♂, J. C. Armstrong. 9343, Nassau, Mar. 1930, 1 ♂, R. W. Miner. 3297, no date, 1 ♂, col. unknown. 11290, Dicks Point, New Providence, 1946-47, 1 ♂, H. Dodge. 11297, Octagon Point, New Providence, 1946-47, 1 ♀, H. Dodge. 2252, Andros, no date, 3 ♂, B. E. Dahlgren and H. Müeller. 959, Andros, Apr. 1908, 7 ♂, 1 ♀, B. E. Dahlgren and H. Müeller.

CUBA

3158, 6 mi SW Cienfuegos, off Cayo Carenas [22°05′N, 80°28′W], 18 June 1918, 1 ♂, B. Brown. 3165, Cayo Cristo [23°03′N, 80°00′W], 4 mi N Isabela, 2-3 July 1918, 1 ♀, B. Brown.

HAITI

11219, Bizoton Reef [18°32′N, 72°23′W], 4 Mar. 1927, 1 ♂, 2 ♀, W. Beebe Exped.

PUERTO RICO

2671, near San Antonio Bridge, San Juan, 10 July 1914, 1 ♂, 1 ♀, R. W. Miner. 2674, Landing place in Candado Bay, San Juan, 9 July 1914, 1 ♀, R. W. Miner. 2682, San Juan Harbor, 21 July 1914, 1 ♀ (ov), R. W. Miner. 2672, rocks at entrance of Condado Bay, San Juan, 14 July 1914, 1 ♀, R. W. Miner.

ZAIRE

3455, no date, 1 ♂ (dry), H. Lang and J. Chapin. 3272 and 3329, Banana, Aug. 1915, 4 ♂, 5 ♀, H. Lang and J. Chapin. 3340, Banana, no date, 6 ♂, 5 ♀, H. Lang and J. Chapin. 3428, Manuba, Banana, July 1915, 2 ♂, H. Lang and J. Chapin. 3476, Banana, July 1915, 1 ♀ (juv), H. Lang and J. Chapin.

ANGOLA

3443, Luanda, 23 Sept. 1915, 1 ♀, H. Lang and J. Chapin. 5895 [Angola ?], 1925, 6 ♂, 2 ♀ (1 ov), Vernay Angola Exped. 5901, [Angola ?], 1925, 3 ♂, Vernay Angola Exped. 5884, Lobito Bay, Apr. 1925, 1 ♀, H. Lang and R. Boulton. 5882, Lobito Bay, May 1925, 7 juv (frags.), H. Lang and R. Boulton.

ANSP. 4 lots, 4 specimens.

UNITED STATES

Florida: 3569, Manatee R. [Manatee Co.], no date, 1 ♂, S. Ashmead.

VIRGIN ISLANDS

St. Croix: 3485, no date, 1 ♀ (dry), R. E. Friffith.

ST. MARTINS

1316, no date, 1 ♂, Van Rijgersma.

[ST. BARTHÉLEMY]
621, Bartholemew I., no date, 1 ♂, A. Goes.

BMNH. 10 lots, 18 specimens.

UNITED STATES
Florida: 1938.3.19.21, Dry Tortugas, 2 ♂, Colman and Tandy.

JAMAICA
1960.8.25.1, Portland Bight, 18 May 1956, 1 ♀ (ov), H. M. S. *Vidal*.

MEXICO
65.29, 2 ♂, (dry), vi/9.

BRAZIL
48.86, 1 ♂, (dry), vi/6/7. Pernambuco, unreg. 1 ♂, D. Wilson Barker.

GAMBIA
Unreg., Gunjur beach, 13 Nov. 1950, 1 ♂ (juv), M. H. Routh. 1952.9.9.21/22, 1 mi N Gunjur, 3 Mar. 1951, 1 ♀, and Rock pool N end Gunjur beach, 11 Dec. 1950, 1 juv, M. H. Routh.

SIERRA LEONE
1920.9.21.1/5, Murray Town, 2 ♂, 3 ♀, W. P. Lowe.

FERNANDO PÓO
53.1, 1 ♂ (dry), vi/9, Cuming.

ANGOLA
1911.2.28.14/15, Luanda, 1 ♂, 1 ♀, W. P. Lowe.

MCZ. 27 lots, 71 specimens.

UNITED STATES
Florida: 5208, July 1859, 1 ♀ (ov), Capt. Woodbury. 5148, 13 Feb. 1861, 2 ♂, Capt. Woodbury. 8747, no date, 1 ♂, Maynard. 5149, Key West, Feb. 1859, 1 ♂, T. Lyman. 5150, Key West, no date, 2 ♂, C. E. Faxon. 5209, Fort Jefferson, Tortugas, no date, 2 ♂ (part of Ordway's material).

BAHAMAS
8665, E Great Abaco I., 1904, 1 ♀, Allen, Brant, and Barbour. 11672, Alicetown, North Bimini, May 1941, 1 ♂, 1 juv, R. W. Foster and J. Huntington. 8635 and 8646, Mangrove Cay, Andros I., 1 Aug. 1904, 1 ♂, 1 juv, O. Bryant. 9425, Simms, Long I., 7 July 1936, 1 ♂, Harvard Bahama Exped. 10359, Salt Pond canal, 1.5 mi SE Matthew Town, Great Inagua I., 24 June 1938, 1 ♂, R. A. McLean and B. Shreve.

CUBA
2893, Bahía Honda, 1877-78, 2 juv, *Blake* Exped.

HAITI
5156, near Jérémie, no date, 1 ♂, D. F. Weinland.

DOMINICAN REPUBLIC
9841, Santa Barbara de Samaná, Aug. 1937, 1 ♀, W. J. Clench.

VIRGIN ISLANDS
St. Thomas: 5153 and 8864, Dec. 1871, 20 ♂, 10 ♀ (2 ov), *Hassler* Exped.

TOBAGO
9917, Pigeon Point, 17-18 Aug. 1937, 2 ♂ (juv), E. Deichmann.

CAPE VERDE ISLANDS
6530. La Praia, July 1883, 1 ♀, *Talisman* Exped.

MNB. 4 lots, 8 specimens.

BRAZIL
Ceará: 333, Fortaleza, Praia de Mucuripe, 1945, 1 ♀, A. Carvalho. Pernambuco: 55, [no other data], 3 ♂, 2 ♀. 331, Recife, Praia do Pina, Sept. 1944, 1 ♂. 330, Recife, Praia do Pina, Aug. 1944, 1 ♂.

MNHNP. 13 lots, 18 specimens.

GUADELOUPE
No date, 2 ♂, (dry), M. Beaupertuis.

CAPE VERDE ISLANDS
La Praia, July 1883, 1 ♂, *Talisman*, 41-42. No date, 1 ♂, M. Barboradu Bocage 587-66. No date, 1 ♀, M. Bouvier.

SENEGAL
Beach at Dakar, May 1895, 1 ♀ (ov), M. Chaper.

GUINEA
Fotoba, Isles des Guinée, [6 mi W Conakry], 9-10 Mar. 1947, 2 ♂, 1 ♀, Inst. d'Afrique Noire.

SÃO TOMÉ
Golfe de Guinée, 1956, 1 ♀, *Calypso* Stn. T 28. Golfe de Guinée, 1956, 1 ♀ (ov), *Calypso* Stn. T 9.

GABON

Types, 3 ♀ (dry). 3 juv, M. Duparquet 181.63 (dry).

CONGO

1892-94, 2 ♀, Dybowski.

RMNH, 38 lots, 105 + specimens.

UNITED STATES

Florida: 23268, Bear Cut, Key Biscayne, 1 Jan. 1965, 2 ♂ (juv), J. A. Cabreru and L. B. Holthuis. 18719, Bear Cut, Key Biscayne, 1-9 Sept. 1963, 1 ♂, L. B. Holthuis. 15003, Tortugas, July 1925, 1 ♂ (juv), H. Boschma.

BAHAMAS

6911 and 11859, Nassau, New Providence I., 1887, 1 ♂, 1 ♀, A. de Haas. 1860, Bahama Is., 1887, many adults, A. de Haas.

VIRGIN ISLANDS

15009, St. Croix, Krause Lagoon, 15 June 1955, 2 juv, P. W. Hummelinck.

ST. MARTIN

11861, coast near Philipsburg, 16-17 Feb. 1957, 1 ♂, 4 juv, L. B. Holthuis. 11866, Freshwater pond W of Philipsburg, 17 Feb. 1957, 6 ♂, 2 ♀, 9 juv, L. B. Holthuis. Unnumbered, mouth freshwater pond W of Philipsburg, 17 and 20 Feb. 1957, dry carapace, L. B. Holthuis. 10720, Great Bay, 7 June 1950, 1 ♂, T. W. Hummelinck. 8121, Great Bay, Ft. Blanche, 26 June 1949, 1 juv, T. W. Hummelinck. 11864, Oyster pond on E coast, 22 Feb. 1957, 1 ♂, 1 ♀, L. B. Holthuis. 1128, NE shore Great Bay, 16 May 1949, 2 ♀, P. W. Hummelinck.

GUADELOUPE

23423, Grande Anse by bridge, La Desirade, 23 Jan. 1964, 1 ♂, P. W. Hummelinck.

ARUBA

11863, Lagoon W Savaneta, 19 Mar. 1957, 2 ♂, L. B. Holthuis. 15008, Lagoon NW Savaneta, 21 Mar. 1957, ♂ juv, L. B. Holthuis. 557, 1881-1882, 6 ♂, 3 ♀, A. J. van Koolwijk. 11862, 1883, 1 ♀, K. Martin. 1872, July 1883, 3 ♂, 1 ♀ (juv), de Haas. 2273, June 1920, 1 ♂ (juv), Prof. col.

CURAÇAO

15006, Santa Cruz Baai, 13 Nov. 1956, 1 ♀ (juv), L. B. Holthuis. 15004, Piscadera Baai, 14 Nov. 1957, 2 ♀ (juv), L. B. Holthuis. 11865, Piscadera Baai, 11-13 Feb. 1957, 2 ♂, 1 ♀, L. B. Holthuis. 23422, SE part Piscadera Baai, 25 Oct. 1963, 1 ♂, P. W. Hummelinck. 23401, S part Piscadera Baai, 25 Oct. 1963, 1 ♀, P. W. Hummelinck. 11860, Mouth of Piscadera Baai, 19 Dec. 1956, 1 ♀, 2 juv, L. B. Holthuis. 23459, Mouth of Piscadera Baai, 14 Dec. 1963, 1 ♀ (paper shell), P. W. Hummelinck. 15015, Mouth of Spanish Water near Nieuwpoort, Santa Barbara beach, 25 Nov. 1956, 1 ♂, L. B. Holthuis. 15005, Mouth of Spanish Water near Nieuwpoort, Santa Barbara beach, 8-13 Nov. 1957, 1 ♂, 4 juv, L. B. Holthuis. 18644, Boca Grandi, St. Jean, 6 Feb. 1955, 2 ♂, J. S. Zaneveld. 15007, S shore St. Joris Baai near Choloma, 3 Jan. 1957, 2 ♂, 1 ♀, 1 juv, L. B. Holthuis. 18646, back part Playa Grandi, Boca Wacao, 30 Jan. 1955, 1 ♂, juv, J. S. Zaneveld. 15010, Spanish Water near Jan Zoutvat, 18 Nov. 1956, 1 ♂, juv, L. B. Holthuis. Unnumbered, reefwater, June 1920, 1 ♀ (ov?), Boeke.

BONAIRE

Lagoon, 27 Mar. 1955, dry carapace, mature, J. S. Zaneveld and R. W. Hummelinck. 11867, Lagoon on E coast, 10 Mar. 1957, 3 ♂, 1 ♀, 4 juv, L. B. Holthuis.

NIGERIA

Lagos Harbor, 23 May 1964, 1 carapace (dry), *Pillsbury* Stn. 1.

SADZ-B. 7 lots, 11 specimens.

UNITED STATES

Florida: 878, Key West, 1885, 1 ♂, Smithsonian.

BRAZIL

Ceará: 3231, Fortaleza, Praia de Iracema, 21 Jan. 1964, 3 ♂, A. L. Castro. Bahia: 3215, Ilha Madre de Deus [12°44′S, 38°37′W], 1932, 1 ♂, Oliviera Pinto. 1731, Ilha Madre de Deus, Jan. 1933, 1 ♂, Pinto e Camarão. 3224, Ilhéus, 1919, 3 ♂, E. Garbe. Rio de Janeiro: Unnumbered, Angra dos Reis, Praia Mombaca, 1 ♀. São Paulo: 890, São Sebastião, 1915, 1 ♂, E. Garbe.

UNC-IMS. 4 lots, 6 specimens.

UNITED STATES

North Carolina: Back Sound off mouth of Taylor Creek, Carteret Co., 20 Nov. 1971, 1 ♀, C. A. Johnson III.

CONGO

2740, Pte. Indienne, env. de Point-Noire, 12 May 1964, 1 ♂, 1 ♀, A. Stauch. 2741, Pte. de Tchitembc, 31 Dec. 1963, 1 ♀ (ov), A. Stauch. 2742, W de Pointe-Noire, 1 ♂, 1 ♀, A. Crosnier.

Supplementary literature records.— Bermuda (Verrill, 1908a); Veracruz, Mexico (Contreras, 1930); Aruba (de Man, 1883); Los Roques and La Orchila, Venezuela (Chace, 1956); Barra das Jangadas, S of Recife, Brazil (Coêlho, 1966); near Rio de Janeiro, Brazil (Oliveira, 1956); Ilha da São Sebastião, Brazil (Luederwaldt, 1929); Port Etienne, Mauritania, and Apam, [Ghana], plus a long list of localities duplicated in material examined and other literature (Monod, 1956); Cape Verde Islands (2 localities), and Angola (3 localities) (Guinot and Ribeiro, 1962); Bissau, Portuguese Guinea (Osorio, 1887, 1888, 1898); Gold Coast (Buchanan, 1958); São Tomé (Forest and Guinot, 1966); Pointe Noire, Congo (Rossignol, 1962).

CALLINECTES SIMILIS WILLIAMS
Lesser Blue Crab

Figures 4, 18b, 20c, 22a, 24

Callinectes ornatus.- Ordway, 1863, p. 572 (part, the Texas specimen).- Rathbun, 1896, p. 356 (part).- 1930, p. 114 (part).- Hay and Shore, 1918, p. 433, pl. 34, fig. 2.- Contreras, 1930, p. 231 (part), fig. 4 (?).- Pounds, 1961, p. 42, pl. 7, fig. 2c.- Williams, 1965, p. 172, fig. 152.

Callinectes danae.- Rathbun, 1930, p. 118 (part).- Pounds, 1961, p. 42, pl. 7, fig. 2b.

Callinectes similis Williams, 1966, p. 87, figs. 3, 4E, F (type: ♂, USNM 113341, 2-3 mi off beach between St. Johns River jetties and Jacksonville Beach, Fla.).

Description.—Carapace (Figure 4) with four frontal teeth, submesial pair small but definitely formed. Central trapezoidal (metagastric) area short and wide, anterior width about 2.75 times length, posterior width about 1.6-1.7 times length. Anterolateral margins broadly arched; anterolateral teeth exclusive of outer orbital and lateral spine short and broad, tips of first five nearly rectangular, sixth and especially seventh acuminate; first five teeth with anterior margins shorter than posterior and separated by narrow based rounded notches. Lateral spine strong, slender, and curved forward. Surface of carapace even, lightly and quite uniformly granulate except smooth along posterolateral and posterior slopes, and nearly smooth along anterolateral and anterior margins, especially between teeth and along orbits; smooth areas with tendency to iridescence.

Chelipeds with very fine granulations on ridges; carpus bearing two obsolescent granulate ridges and suggestion of others, inferior lateral ridge terminating anteriorly in a low tooth occasionally followed by a low flattened eminence; chelae strong, not greatly dissimilar in size.

Male telson longer than wide; sixth segment of abdomen slightly sinuous sided but broader at all levels than telson, proximal half slightly constricted laterally and less indurated than other parts, flush with sternum in retracted position. Mature female telson slightly wider than long. First gonopods of male (Figures 18b, 20c) reaching anteriorly two-thirds length of sternite VII, or beyond; distal portion slender, extending straight to tips curved slightly mesad, armed with scattered minute retrogressive spinules, most dense distally and laterally and largest distally. Gonopores of female (Figure 22a) narrowly ellipsoid with long axis in transverse plane; aperture of each with simple rounded borders except at mesial end where it slopes from surface laterad under superior anterior margin.

Size of carapace in mm.—Largest male: length 55, width at base of lateral spines 97, including lateral spines 122. Largest female: length 45, width at base of lateral spines 76, including lateral spines 95. Summary of selected measurements is given in Tables 1 and 2. Franks et al. (1972) reported an individual with carapace width of 171.

Color.—Adult male: "Carapace green dorsally, irregular areas of iridescence at bases of, and between, anterolateral teeth, and on posterior and posterolateral borders. Chelipeds and portions of legs similar in color or more tannish green dorsally, with iridescent areas on outer and upper edges of carpus and hands; chelae white on outer face, blue to fuchsia on inner surface, with fuchsia on tips of fingers and teeth of opposed edges. Lateral spines and some anterolateral teeth, as well as spines on chelipeds, white tipped. Walking legs grading from fuchsia distally through violet blue to light blue mottled with white proximally,

pubescence on legs beige. Swimming legs variably mottled with white; all legs with stellate fuchsia markings at articulations. Underparts white and blue." (Williams, 1965).

Ovigerous female: "Similar to male except with more violet blue on inner surface of chelae; fingers either with white teeth or fuchsia colored teeth. Legs with dactyls reddish orange grading abruptly to blue on propodi, pubescence brown to beige. Abdomen with iridescent areas." (Williams, 1965).

Carapace of juveniles sometimes with a maculate light olive pattern.

Variation.—Borders of the metagastric area are somewhat more deeply defined on young individuals than adults, and the shape of this area tends toward that in *C. danae* (USNM 123015, Mississippi) in the young. Differentiation of the major and minor chelae resembles that in other members of the genus although the two chelae on most individuals tend to be similar sized. In some specimens the major chela has a strong proximal tooth on the dactyl.

Habitat.—Franks et al. (1972) gave a good summary of habitat for this species. In Mississippi they caught it year round in trawl samples from 9- to 92-m depths at temperatures ranging from 13.2° to 29.0°C and in salinities ranging from 24.9 to 37.4‰, but it was most abundant in 37-m depths and showed a slight preference for 29.0 to 31.9‰ salinities. The same environment exists in northeastern Florida where Tagatz (1967) found the species most abundant in the ocean near shore and in the lower 25 miles of St. Johns River, mainly in salinities greater than 15‰; also in North Carolina it is seldom found in estuaries beyond lower limits of 15‰ salinity. In all areas studied the species is associated with *C. sapidus*, often in large numbers, but it is usually culled out of commercial catches because of its small size (Lunz, 1958; Pounds, 1961; Williams, 1966; Franks et al., 1972).

Spawning.—Published data on spawning in Texas and South and North Carolina summarized by Williams (1966) suggested a spring and fall spawning season for *C. similis*, and Tagatz (1967) found this true for northeastern Florida as well where females spawn in the ocean from March to July, peaking in May when 75% of them are ovigerous, and again from October to November. Ovigerous females in the collection of the USNM indicate that these limits are somewhat broader elsewhere and may be correlated with temperature, for there are representatives from Louisiana and Texas in February and Campeche Banks in December.

Distribution.—Off Delaware Bay to Key West, Fla.; northwestern Florida around Gulf of Mexico to off Campeche, Yucatán (Figure 24).

Remarks.—Small- to medium-sized juveniles are extremely difficult to identify in parts of the range where *C. danae* and *C. ornatus* also occur (southern Florida).

The few specimens from off Delaware Bay are all juveniles, suggesting that northern limits for this species, as for many others from the Carolinian Province, vary seasonally and are extended northward during favorable warm years.

Among unusual specimens seen, a female taken off Cape San Blas, Fla. (USNM 101429) with carapace measuring 37 mm long × 64 mm wide, exclusive of lateral spines, bears dorsally the largest *Chelonibia* seen fouling the species. The barnacle measures 18.5 × 21.3 mm at base × 18.3 mm height of sidewall. An immature female crab taken off Timbalier Bay, La. (USNM 123026) has that part of the front bearing frontal teeth produced forward.

Closely resembling *C. danae* and *C. ornatus*, *C. similis* seems to be the Carolinian member of the complex. *Callinectes similis* has the smoothest and most uniformly granulated carapace among the three, and the shortest, broadest anterolateral teeth. These teeth are not equilaterally triangular, having shorter anterior than posterior borders, and are more directed forward in the anterior portion than in the remainder of the row. Central teeth in the row have the anterior border extending almost straight laterad. The carapace of mature females has very little sculpture and remarkably uniform granulation overall. Granulations on the ridges of the chelipeds are among the finest of any species of *Callinectes*. Because of simplicity in structure of the male first gonopods, the relatively broad male abdomen and relatively generalized structure of the chelae and frontal teeth, it is tempting to regard this species as one of the most primitive or unspecialized members of the genus and I have arranged it so in the order of presentation, knowing full well that such evidence is highly subjective.

Material.—Total: 117 lots, 354 specimens.

USNM. 104 lots, 329 specimens, including the following listed in Rathbun (1930) as *C. danae* (20115, 22817), *C. marginatus* (33103), and *C. ornatus* (8863, 62460, 58366, 3185, 51029, 61428, 21631).

UNITED STATES

New Jersey: 62674, Cape May, 8 Sept. 1928, 1 ♂ (juv), H. G. Richards. 64257, near Brandywine Lightship, Delaware Bay, 29 July 1930, 1 ♂ (juv), H. G. Richards. 77009, off New England Creek, Delaware Bay, 25 Aug. 1931, 1 ♀ (juv), H. G. Richards.

Delaware: 77008, off Slaughter Creek, 4 Aug. 1931, 1 juv, H. G. Richards.

North Carolina: 123058, Beaufort, recd. 19 Nov. 1959, 1 ♀ (ov), J. D. Costlow, reared larvae. 123059, Beaufort Harbor, Aug. 1946, 1 ♂, D. H. B. Ulmer.

South Carolina: 97699, N Edisto R., 22 Apr. 1953, 1 ♂, 7 ♀, G. R. Lunz. 123012, S Creek near entrance into N Edisto R., 31 May 1966, 1 ♂ (juv), J. C. McCain. 123011, off mouth N Edisto R., 31 May 1966, 1 ♀, J. C. McCain.

Georgia: 123054, Jointer R. [near Jekyll I.], 17 Mar. 1932, 2 ♀, W. W. Anderson.

Florida: 123034, [off mouth St. Johns R.], 30°26.5′N, 81°23′W, 17 Apr. 1940, 9 ♂, 9 ♀ (6 juv), *Pelican* Stn. 215-1. 123047, [off mouth St. Johns R.] 30°26′N, 81°20.5′W, 17 Apr. 1940, 1 ♂, 1 ♀, *Pelican* Stn. 215-2. 113345, off St. Johns R. jetties, 14 Aug. 1962, 8 ♂, 6 ♀, M. E. Tagatz and G. P. Frymire. 113341, 113342, 113343, 113344, 2-3 mi off beach between St. Johns R. jetties and Jacksonville Beach, 18 June 1962, 8 ♂, 9 ♀, A. B. Williams et al. 123014, [off Jacksonville Beach] 30°21′N, 81°20.5′W, 19 Nov. 1963, 2 ♂, 2 ♀, *Silver Bay* Stn. 5381. 123101, [off St. Augustine] 29°54.5′N, 10°10′W, 9 Feb. 1965, 2 ♀, *Oregon* Stn. 5234. 123018, [off SE St. Johns Co.] 29°28.5′N, 81°04.5′W, 28 Mar. 1940, 2 ♂, *Pelican* Stn. 202-6. 99917, Matanzas R. at Crescent Beach, 1 Dec. 1954, 1 ♂, D. K. Caldwell. 123017, [N Daytona Beach] 29°18.5′N, 81°01.5′W, 6 Apr. 1940, 1 ♀, *Pelican* Stn. 212-3. 123046, [off Daytona Beach] 29°14.5′N, 80°59.5′W, 6 Apr. 1940, 1 ♂, 1 ♀ (ov), *Pelican* Stn. 212-2. 123020, [off Daytona Beach] 29°07.5′N, 80°55′W, 5 Apr. 1940, 5 ♂, 2 ♀, *Pelican* Stn. 211-5. 123021, [off Daytona Beach] 29°11′N, 80°43′W, 19 Jan. 1940, 1 ♀, *Pelican* Stn. 172-3. 123008, 123009, Ponce de Leon Inlet, Volusia Co., 13 Apr. 1946, 2 ♂ (juv), DePalma and Strickland. 123045, [off New Smyrna] 29°00′N, 80°47.5′W, 19 Jan. 1940, 1 ♂, *Pelican* Stn. 171-7. 101686, NE off Cape Canaveral, 29°15′N, 80°13′W, 1 June 1957, 2 ♀ (1 ov), *Combat* Stn. 334. 123016, [off Cape Canaveral] 28°24′N, 80°32.5′W, 4 Apr. 1940, 1 ♂, *Pelican* Stn. 207-3. 123022, [SE Cape Canaveral] 28°23′N, 80°27.5′W, 18 Jan. 1940, 1 ♂, *Pelican* Stn. 169-2. 99902, Sewall Point, Martin Co., 27 Feb. 1955, 2 juv, D. K. Caldwell et al. 113460, Bear Cut Key, Biscayne side Miami, 17 Aug. 1965, 1 ♂, 1 ♀ (juv), R. B. Manning. 77103, Coral Gables, 7 July 1932, 1 ♂, J. F. W. Pearson. 76984, Key West, 26 May 1918, 1 ♂ (ov), 3 juv., D. R. C. 76980, Key West, no date, 2 ♀, C. H. Maynard. 123103, mud cove 2 mi from tip of Alligator Harbor, Franklin Co., 27 Oct. 1967, 4 ♂, 5 ♀, C. Swift and J. Rudloe. 101429, off Cape San Blas, 29°16′N, 85°08′W, 15 July 1957, 1 ♀ (ov), *Oregon* Stn. 1755. 123102, St. Andrews Bay Shipyard area, Bay Co., 18 Aug. 1967, 1 ♂, L. Abele and C. Swift. 99914, Choctawhatchee Channel, Okaloosa Co., no date, 1 ♀, K. Caldwell. 99896, Intracoastal Waterway 3.5 mi E Interarity Point, Pensacola, 15 Aug. 1953, 1 ♂, F. Berry and A. Mead.

Alabama: 92425, 30°15.5′N, 88°10′W, 22 June 1951, 3 ♂, 1 ♀, 1 juv., H. M. Hefley, *Oregon* Stn. 387.

Mississippi: 123015, inside Petit Bois Island, Mississippi Sound, 20 Apr. 1967, 27 ♂, 10 ♀, *George M. Bowers* Stn. 4. 123010, off N side Little Deer Island, Ocean Springs, 1 Sept. 1965, 3 juv, J. C. McCain.

Louisiana: 123040, 28°22.5′N, 91°44.5′W, 12 July 1938, 1 ♂, *Pelican* Stn. 84-1. 123057, 28°31′N, 91°09′W, 13 July 1938, 3 ♂, 1 ♀ (juv), *Pelican* Stn. 86-4. 123029, 28°38′N, 91°05′W, 18 Mar. 1938, 1 ♂, *Pelican* Stn. 31. 123019, 28°39.5′N, 91°06′W, 11 Nov. 1938, 1 ♂, 2 ♀ (1 juv), *Pelican* Stn. 90-2. 123039, 28°40′N, 90°51.5′W, 10 July 1938, 1 ♂ (juv), *Pelican* Stn. 80-7. 123035, 28°41.5′N, 91°10′W, 11 Nov. 1938, 2 ♂, 2 ♀ (1 juv), *Pelican* Stn. 90-3. 123050, 28°42′N, 92°15.5′W, 13 Nov. 1938, 4 ♂, 4 ♀, *Pelican* Stn. 93-6. 101428, 28°46′N, 90°47′W, 6 Mar. 1957, 7 ♀ (ov), *Oregon* Stn. 1749. 123033, 28°46.5′N, 91°18.5′W, 11 Nov. 1938, 1 ♂, *Pelican* Stn. 90-5. 123037, 28°48′N, 89°51′W, 13 May 1938, 3 ♀ (2 ov), *Pelican* Stn. 69-6. 123048, 28°49′N, 91°23′W, 11 Nov. 1938, 3 ♂, 1 ♀, *Pelican* Stn. 90-6. 92350, 28°50′N, 89°33′W, 7 May 1951, 1 ♂, *Oregon* Stn. 342. 91432, 28°53.3′N, 89°36.5′W, 13 Sept. 1950, 1 ♀ (juv), *Oregon* Stn. 107. 123038, 25 mi S Grand Isle, 28°55′N, 90°02′W, 17 Feb. 1938, 1 ♂, *Pelican* Stn. 22. 123041, 28°55′N, 92°15.5′W, 13 Nov. 1938, 3 ♂, *Pelican* Stn. 93-3.

123025, 28°55.5′N, 89°59′W, 10 Nov. 1938, 2 ♀ (1 ov), *Pelican* Stn. 87-7. 123028, 28°56′N, 91°52′W, 29 Mar. 1938, 1 ♂, 2 ♀, *Pelican* Stn. 37. 123056, 28°56.5′N, 91°50′W, 11 July 1938, 2 ♂, 2 ♀, *Pelican* Stn. 82-5. 91939, 28°57′N, 89°36′W, 14 Sept. 1950, 1 ♀, *Oregon* Stn. 110. 123036, 28°57′N, 89°43′W, 10 Nov. 1938, 4 ♀ (1 ov), *Pelican* Stn. 87-4. 123024, 28°58′N, 89°28.5′W, 10 Nov. 1938, 1 ♂, *Pelican* Stn. 87-1. 123026, 28°58′N, 90°17′W, 10 July 1938, 1 ♀ (juv), *Pelican* Stn. 79-7. 123023, 28°59′N, 92°15.5′W, 13 Nov. 1938, 1 ♂, 2 ♀ (juv), *Pelican* Stn. 93-2. 123049, 28°59.5′N, 91°44.5′W, 12 Nov. 1938, 1 ♂, *Pelican* Stn. 91-4. 64148, off Breton Island, Nov. 1930, 1 ♂, Stewart Springer. 91954, 29°22′N, 88°49′W, 24 Sept. 1950, 3 ♂, *Oregon* Stn. 132. 123027, 29°01.5′N, 89°33′W, 8 July 1939, 1 ♂, 1 ♀, *Pelican* Stn. 77-2. 91433, 29°12′N, 88°50′W, 12 Sept. 1950, 1 ♂, *Oregon* Stn. 103. 123055, 3-6 mi ESE SW Pass, 16 Feb. 1934, 1 ♀ (ov), T. C. P., M. J. Lindner, and W. W. Anderson.

Texas: 123030, 29°00′N, 94°38.5′W, 21 Jan. 1939, 1 ♀, *Pelican* Stn. 104-5. 123031, 29°10.5′N, 94°50.5′W, 3 May 1938, 5 ♂, 2 ♀, *Pelican* Stn. 56-5. 123005, Galveston, 11 Aug. 1940, 4 ♂, 1 ♀, from J. L. Baughman. 123006, Galveston, 7 July 1940, 1 ♂, 2 ♀ (juv), from J. L. Baughman. 123007, Galveston, 11 Aug. 1940, 9 ♂, 2 ♀ (1 soft), from J. L. Baughman. 80662, Galveston, no date, 5 ♂, 4 ♀, J. L. Baughman. 123013, 17 mi S, 7 mi E Alvin, Brazoria Co., 28 July 1952, 1 ♀ (juv), S. Alvin. 22817, Alligator Head, Matagorda Bay, no date, 1 ♂ (dry), from J. D. Mitchell. 123051, 27°59′N, 95°20.5′W, 22 Jan. 1939, 1 ♀, *Pelican* Stn. 107-3. 123032, 28°20.5′N, 96°13′W, 2 May 1938, 1 ♀ (juv), *Pelican* Stn. 54-2. 101678, 28°20′N, 94°97′W, 25 Sept. 1957, 2 ♀, *Silver Bay* Stn. 187. 123044, 27°40′N, 96°34′W, 22 Apr. 1938, 1 ♂, 2 ♀ (ov), *Pelican* Stn. 42. 123043, 27°51′N, 96°55.5′W, 2 May 1938, 3 ♂, 2 ♀ (1 ov), *Pelican* Stn. 53-1. 80663, Port Aransas Pass, 5 June 1941, 1 ♀, G. Gunter. 80664, Port Aransas Pass, no date, 10 ♂, 11 ♀, G. Gunter. 123042, 26°48.5′N, 96°40′W, 4 Feb. 1939, 1 ♀ (ov), *Pelican* Stn. 115-3. 123052, 26°05′N, 97°05′W, 5 Feb. 1939, 1 ♀ (juv), *Pelican* Stn. 118-4.

MEXICO

Tamaulipas: 94452, 24°12′N, 97°17′W, 13 Oct. 1952, 1 ♀, *Oregon* Stn. 662. 123053, off Soto la Marina, 140 mi S Rio Grande R., 15 Mar 1947, *Pelican*. Campeche Bank: 94453, 19°54.1′N, 91°43′W, 10 Dec. 1952, 1 ♀ (ov), *Oregon* Stn. 719. 94454, 20°12′N, 91°40′W, 11 Dec. 1952, 2 ♂, 1 ♀ (ov), *Oregon* Stn. 720.

AHF. 4 lots, 13 specimens.

UNITED STATES

Florida: Choctawhatchee Bay entrance W end Destin bridge [Okaloosa Co.], 19 June 1949, 6 ♂, 4 ♀, LM42-49.

Louisiana: Breton Sound, Mississippi Delta, 21 Oct. 1951, 1 ♂, R. H. Parker.

Texas: 1.25 mi off Mustang Island, 31 Aug. 1951, 1 ♀, E. Puffer, J498. Off Padre Island, 9 June 1956, 1 ♀, R. H. Parker, J482.

AMNH. 3 lots, 4 specimens.

UNITED STATES

Florida: 11298, Lake Worth, July and Aug. 1945, 1 ♀, W. G. Van Name and A. H. Verrill.

Texas: 2755, Galveston, no date, 2 ♂ (juv), col. unknown.

BAHAMAS

2445, Nassau, 1899, 1 ♂, R. P. W.

BMNH. 1 lot, 1 specimen.

UNITED STATES

Texas: 11.1.1946, 1 ♀, Baughman.

MCZ. 4 lots, 5 specimens.

UNITED STATES

North Carolina: 11352, 2 mi SE Roanoke Island, 19 Dec. 1940, 1 ♂ (juv), R. Foster.

Florida: 5207, 1859, 2 ♂, G. Wurdemann. 5129, Cape Florida (S end Biscayne Bay), no date, 1 ♂ (juv), G. Wurdemann.

Texas: 5134, 13 Feb. 1861, 1 ♂, G. Wurdemann.

RMNH. 1 lot, 2 specimens.

UNITED STATES

Mississippi: 17825, 29°38.5′N, 88°30′W, 21 Aug. 1962, 1 ♂, 1 ♀, *Oregon* Stn. 3713.

UNC-IMS. 7 lots, 74 specimens + many uncatalogued.

UNITED STATES

North Carolina: 1556, (Paratypes), off Beaufort Inlet, Carteret County, 31 Oct. 1962, 5 ♂, 4 ♀ (2 ov), E. Bayer, from *Ensign*.

Florida: 2140, Clapboard Creek, trib. of St. Johns River, 7 June 1964, 7 juv, col. unknown.

2237, Sisters Creek at Fort George River?, Duval County, 2 ♂, 2 ♀, G. P. Frymire and G. C. Williams. 2138, Mouth of Sisters Creek off St. Johns River, M. E. Tagatz and G. P. Frymire. 1995 (Paratypes), off St. Johns River jetties, 5 ♂, 4 ♀, 3 juv, M. E. Tagatz and G. P. Frymire. 1990 (Paratypes), 2 to 3 mi off beach between St. Johns River jetties and Jacksonville Beach, 17 ♂, 16 ♀ (10 ov), 8 juv, G. P. Frymire, M. E. Tagatz, and G. C. Williams.

Texas: 2139, Galveston Bay, June 1964, 1 ♂, col. unknown.

Supplementary literature records.—Laguna Madre de Tamaulipas (as *danae*, Hildebrand, 1957).

CALLINECTES GLADIATOR BENEDICT

Marine Blue Swimming Crab

Figures 5, 18c, 20b, 22c, 24

Lupa smythiana Leach (nomen nudum) in White, 1847, p. 27.

Callinectes tumidus var. *gladiator* Benedict, 1893, p. 537 (type: ♂, USNM 14879, Baya River, Elmina, Ashanti [Ghana]).

Callinectes tumidus gladiator.- Rathbun, 1896, p. 360.

Callinectes gladiator.- Rathbun, 1897, p. 150.- 1900a, p. 291.- 1921, p. 397, fig. 3; pl. 19, fig. 2.- Balss, 1921, p. 58.- Monod, 1927, p. 606.- 1956, p. 205, figs. 236-237.- Irvine, 1932, p. 15, fig. 9.- 1947, p. 298, fig. 203.- Vilela, 1949, p. 58, fig. 6.- Capart, 1951, p. 130, fig. 46.- Rossignol, 1957, p. 82.- 1962, p. 116.- Guinot and Ribeiro, 1962, p. 48.- Crosnier, 1964, p. 32.- Forest and Guinot, 1966, p. 64.

Description.—Carapace (Figure 5) bearing four frontal teeth, submesial pair almost never more than half length of lateral pair. Metagastric area short, anterior width about 2.5 times length, posterior width about 1.5 times length. Anterolateral margins arched slightly; teeth, exclusive of outer orbital and lateral spine, with tendency to arrangement in a 3-2-2 pattern; proximal three narrow-acute and separated by narrow sinuses; middle two broader, acuminate, and more widely separated; lateral two spiniform and trending forward. Lateral spine usually long and slender. Surface finely or moderately and evenly granulate except for variably smooth portions at periphery, especially on posterior and posterolateral slopes. Tendency toward ridging or heaping of granules on branchial and cardiac lobes. Epibranchial line prominent and nearly uninterrupted.

Chelipeds with propodus sharply ridged, ridges granulated; carpus often with granulated ridges evident dorsally; major chela with strong tooth at base of dactyl.

Male abdomen and telson narrow, reaching slightly beyond suture between thoracic sternites IV and V; telson about 1.6 times longer than wide; sixth segment constricted at midlength, sides markedly divergent proximally. Mature female abdomen and telson reaching same level as in male, telson a bit wider than long, sixth segment slightly shorter than fifth. First gonopods of male (Figures 18c, 20b) reaching slightly beyond midlength of thoracic sternite VII; curved sigmoidally in distal half, overlapping, divergent except at extreme tip and twisted mesioventrally on axis; armed distally with minute retrogressive spinules, scattered or occasionally arranged in rows. Gonopores of female (Figure 22c) irregularly lunate with superior limb of each directed anteromesad; aperture of each with rounded margin becoming lowest mesially where it slopes from near surface level laterad under posteriorly arched anterior border.

Size of carapace in mm.—Largest male: length 48, width at base of lateral spines 92, including lateral spines 117. Largest female: length 60, width at base of lateral spine 108, including lateral spines 138. Summary of selected measurements is given in Tables 1 and 2.

This species shows considerable variability in size but is, on the whole, the smallest in the genus. Females are often quite delicate, maturing at sizes as small as a length of 23, width at base of lateral spines 41, and width including lateral spines of 54. Irvine (1947) noted that large individuals measure 6 inches or more (155 mm) across the carapace.

Color.—Uniform gray-green or gray-blue with spot of blue on palm and proximal internal part of fingers of chela (Rossignol, 1962). Beautiful mottled carapace with bright blue legs, called the marine or deep sea blue swimming crab (Irvine, 1932, 1947). Preserved specimens often have an oval dark mahogany colored spot, variable in size, on the gastric and metagastric areas.

Variations.—In some ways *C. gladiator* resembles the "acutidens" form of *C. sapidus*, surpassing it in development of even more acute, slender spination, and showing variable ridging or cresting of granulations on branchial lobes and mesobranchial regions as well as formation of a transverse ridge of granules on each cardiac lobe. The peaking of granules is apparent at quite small size. In addition, these lobes and regions are often prominent and thrown into somewhat angular planes bordering the contrastingly sunken metagastric area. The second abdominal segment terminates laterally in a spine usually sharper and more prominent than in other species of the genus, especially in young or freshly molted individuals.

The lateral spines of most individuals are relatively the longest among species in the genus. Anterolateral teeth may be bilaterally asymmetrical in number. Tips of the teeth may lie in a nearly straight line providing relatively flat anterolateral arcs. All older individuals have a rounded notch between the first two anterolateral teeth. The lower side of each anterolateral margin becomes hairy at an early age.

Openness of the inner orbital fissure is random, bearing no relationship to age or width of carapace. When the fissure is closed, a V-shaped notch usually remains open on the orbital margin.

First gonopods of males are not completely S-shaped and not overlapping in juveniles; in a few males they extend to the level of a suture between thoracic sternites VI and VII. The first gonopods may be unnaturally splayed in preserved specimens. Abdominal segment 6 is often poorly calcified at midlength in males.

Distribution.—West Africa from Baie de Saint-Jean, 19°27′N, 16°22′W, Mauritania, to Baia do Lobito, Angola (Figure 24).

Habitat.—Longhurst (1958) provided an excellent ecological summary of the West African marine benthos primarily in and off the Sierra Leone River, but elsewhere as well. He found that in shelf regions under the influence of tropical shelf water a characteristic fauna was revealed by otter trawls in each sector investigated; the most important species were the swimming crabs *C. gladiator* and *Portunus validus* Herklots which occur in most hauls together with *Penaeus duorarum notialis* Burkenroad, *P. kerathurus* (Forsskål), *Parapenaeus longirostris* (Lucas), *Panulirus rissonii* (Desmarest), and *Sepia officinalis* Linn. Off the Sulima River [=Moa River, Sierra Leone] occurrence of this fauna corresponded with the inshore *Cynoscion* fauna of demersal fish, with the thermocline as its lower limit. In samples, this fauna extended from Senegal to the Bight of Biafra, the genera *Callinectes, Portunus,* and *Panulirus* occurring in a high proportion of hauls from shallowest to 50 m. Irvine (1947), Rossignol (1962), and Crosnier (1964) essentially said the same, that this coastal marine species lives on the bottom from shore to depths of 30 m on sand, sandy mud, or gravel, sometimes with a mixture of shell fragments (Sourie, 1954a) in warm water.

Both Monod (1927) and Rossignol (1957) remarked on the small size and abundance as well as the rapidity and aggressiveness with which *C. gladiator* moves, the latter saying that it often rests three-fourths buried in a predatory position with only antennae and pincers exposed. In addition to trawl hauls, the crab is captured in nets allowed to hang a few feet from the bottom (Irvine, 1947) and at the surface with dip nets under lights at night.

Though found in estuaries to some extent, these accounts imply that *C. gladiator* is much like *C. similis* of the western Atlantic in ecological association and behavior, and less estuarine than *C. latimanus*.

Spawning.—Museum records provide only an outline of spawning that may go on all year. Records of ovigerous females are: December, Angola; January, Guinea, Liberia, and Cameroon; February, Cameroon; March, Sierra Leone, Congo; April, Ghana; May, Senegal, Sierra Leone, and Nigeria; June, São Tomé; October, Congo.

Economic importance.—No direct statements of economic importance are made in literature. Irvine (1947) reported the flesh and eggs edible and of good quality.

Remarks.—Aside from taxonomic accounts and faunal lists, there is less published information on *C. gladiator* than most *Callinectes*. Like others, larger or older specimens often bear one or more barnacles of the genus *Chelonibia* on the carapace. Teeth of fingers on the major chelae are often worn, and the major hands often seem disproportionately large for the size of the animal. One ovigerous female in the BMNH (unregistered)

from Victory Bay, Cameroon, has two major chelae.

The holotype is an immature male somewhat the worse for wear. The left chela is present but dismembered from the body, as are other legs or parts of legs and the abdomen. The left lateral spine is broken about halfway along its length, and only the left first gonopod remains.

Figures provided by Irvine (9 and 13, 1932; 202 and 203, 1947) are difficult to assign to synonymy with confidence, and both Capart (1951) and Monod (1956) had trouble with them. Figures 13 and 202 could represent either *C. gladiator* or *marginatus*, but 9 and 203 are labelled as *C. gladiator*, yet internal carpal spines on the latter indicate a species of *Portunus*. Since the features are sketchy, it is best to accept the author's designation with allowance for error.

The specimen named by Leach (in White, 1847) is an immature female with prominently ridged areas on the carapace and straight lateral spines typical of *C. gladiator*. There is a small mature female in this same collection.

Material.—Total: 80 lots, 412 specimens.

USNM. 18 lots, 95 specimens.

SENEGAL
21384, Dakar, 3 May 1892, 1 ♂, O. F. Cook. 119469, Dakar Harbor, 25-26 July 1964, 2 ♂, 2 ♀, *Geronimo*.

LIBERIA
20670, Mouth of Mesurado, Monrovia, no date, 1 ♀ juv, O. F. Cook. 87395, Farmington River at Snafu Docks, Nov. 1946, 3 ♂, 1 ♀, H. A. Beatty. 97861 and 97862, off St. Paul River mouth, Monrovia, 6 Jan. 1953, 2 ♀ (ov), G. C. Miller. 97863, off St. Paul River mouth, Monrovia, 4 Mar. 1953, 1 ♂, G. C. Miller.

IVORY COAST
120937, 05°02.5′N, 03°49.5′W, 30 May 1964, 2 ♀, *Pillsbury*.

GHANA
14879, Baya River, Elmina, Ashantee, 1889, 1 ♂, W. H. Brown, Jr., (Type).

NIGERIA
120938, Lagos, 9 May 1965, 1 ♂, *Pillsbury* Stn. 226. 123094, Lagos, 23 May 1964, 18 ♂, 22 ♀, 1 juv, *Pillsbury* Stn. 2. 120939, Lagos, 10 May 1965, 4 ♂, 6 ♀, *Pillsbury* Stn. 229. 120940, 04°06′N, 05°58′E to 04°02′N, 06°04′E, 14 May 1965, 9 ♂, 11 ♀, 1 juv, *Pillsbury* Stn. 250. 120941, 04°04′N, 06°18′E, 14 May 1965, 1 ♀, 1 juv, *Pillsbury* Stn. 252.

FERNANDO PÓO
120942, 03°35′N, 08°48′E, 15 May 1965, 1 juv, *Pillsbury* Stn. 258.

ZAIRE
54251, Banana, mouth of Congo River, Aug. 1915, 1 ♂, 1 ♀, H. Lang. 54252, Banana, mouth of Congo River, no date, 1 ♂, H. Lang.

AMNH. 4 lots, 7 specimens.

ZAIRE
3403 and 3470, Banana, Aug. 1915, 3 ♂, 1 ♀, H. Lang and J. Chapin.

ANGOLA
3385 and 3463, Santo Antonio do Zaire, Aug. 1915, 2 ♂, 1 ♀, H. Lang and J. Chapin.

BMNH. 19 lots, 64 specimens.

GAMBIA
1927.1.27.1, Cape St. Mary, 1 ♂, T. R. Hayes, Sir C. H. Armitage. 1952.9.9.19/20, 1 mi N Gunjur on coast, 1 ♂, 1 ♀, M. H. Routh.

SIERRA LEONE
1955.10.7.35, Rokel estuary [NE Freetown], 1 ♀ juv, T. S. Jones. 1957.5.26.76/78, Banana I., 2 ♂, 2 ♀, A. R. Longhurst. 1922.0.13.1/5, Sherbro I., 5 ♂, 5 ♀ (juv), C. H. Allan.

GHANA
1931.5.21.1, Accra, 1 ♂, F. R. Irvine. Two unreg. lots, Accra, 2 ♂, 3 ♀ (1 ov), F. R. Irvine.

NIGERIA
1966.10.17.3/4, 1 ♂, 1 ♀, Ejike. 1938.8.15.47/48, 5 juv, A. G. Taylor.

CAMEROON
1967.11.4.1/2, Ambas Bay [4°N, 9°10′E], Feb. 1966, 2 ♂, T. S. Jones. 1962.2.1.24/27, Victoria Bay, 4 ♂, 1 ♀, J. T. Swarbrick. Unreg., Victoria Bay, 16 ♀ (3 ov), J. T. Swarbrick. Unreg., Cameroon coast, Mar. 1962, 1 ♂, 1 ♀, R. C. Ward.

WEST AFRICA

Unreg., 22, 1 ♀. Dry coll. vi/9, 1 ♀, Congo Exped., I. Cranch. Unreg., 1♀, *Lupa smythiana* Leach MS, *Neptunus sanguinolentus* in White Catalogue, 1847, J. Cranch.

MNHNP. 11 lots, 27 specimens.

SENEGAL

Rufisque, 11 and 13 May 1947, 2 ♂, T. Monod. M'bour, 1948, 1 ♀, Dekeyser-Villiers. Off M'bour-N'gaparou, May 1949, 2 ♀ (ov), *G. Trêca*, Crémoux.

SIERRA LEONE

Gulf of Guinea, 07°20′15″N, 12°39′W, 1956, 1 ♀ (juv), *Calypso* Stn. 11.

IVORY COAST.

Off Abidjan, 05°16′12″N, 04°0′20″W, 1956, 9 juv, *Calypso* Stn. 20.

CAMEROON

Longji (Kribi)?, 30 May 1956, 1 ♂, *Calypso* Stn. 34. Mouth of the Kienke, Kribi, 1 ♀, T. Monod. Souelaba, 1932, 3 ♂ (juv), T. Monod.

SÃO TOMÉ

Gulf of Guinea, 1956, 1 ♀ (ov), *Calypso* Stn. T27. 3 ♂, 3 juv, *Calypso* Stn. T9.

RMNH. 13 lots, 95 specimens.

LIBERIA

1871, Grand Cape Mount, 1881, 1 ♂, 2 ♀, J. Büttikofer and J. A. Sala.

NIGERIA

24186, Gulf of Guinea, 03°45′N, 08°03′E, 03°45′N, 08°02′E, 14 May 1965, 1 ♀, *Pillsbury* Stn. 256. 23520, off Nigeria, 04°03′N, 06°03′E, 04°04′N, 06°04′E, 14 May 1965, 3 ♂, 5 ♀ (1 ov), *Pillsbury* Stn. 251. 20597, Lagos Harbor, 23 May 1964, juv 5 ♂, 14 ♀, *Pillsbury* Stn. 2. 23519, Lagos Harbor, 10 May 1965, 1 ♂, 2 ♀, *Pillsbury* Stn. 228. 15532, Port Harcourt, Niger Delta, May-Aug. 1960, 4 ♂, H. J. G. Beets.

FERNANDO PÓO

24185, 03°45′N, 08°48′E, 15 May 1965, 1 ♂ (juv), *Pillsbury* Stn. 257.

CAMEROON

21572, Kribi, 9 Aug. 1964, 30+ (juv), B. de Wilde-Duyfies. 21149, Kribi, 9 Mar. 1964, 11 ♂, 4 ♀, B. de Wilde-Duyfies. 21178, Doula, 10 Feb. 1964, 1 ♂, B. de Wilde-Duyfies.

GABON

14995, Port Gentil, 1 juv, J. H. Logeman

CONGO

374, 1880, 1 ♀, 2 juv, T. Kamerman.

ANGOLA

1876, Musserra, 1882, 1 ♂, 1 ♀, T. Kamerman.

UNC-IMS. 15 lots, 125 specimens.

TOGO

2717, 06°06′30″N, 01°37′30″E, 16 Oct. 1963, 1 ♀, A. Crosnier.

DAHOMEY

2718, 06°19′N, 02°24′E, 20 July 1964, 1 ♂, 2 ♀, A. Crosnier.

CAMEROON

2719, 03°55′N, 09°00′E, 5 Jan. 1963, 3 ♀ (2 ov), A. Crosnier. 2720, 03°32′N, 09°35′E, 24 Aug. 1963, 5 ♂, 5 ♀, A. Crosnier.

GABON

2721, Baie de Corisco, near Libreville, 3 July 1960, 1 ♂.

CONGO

2722, off Pointe-Noire, Mar. 1962, 4 ♂, 1 ♀ (ov), A. Crosnier. 2723, Beach and Bay at Pointe-Noire, Oct. 1963, 6 ♂, 10 ♀ (5 ov), A. Crosnier. 2724, 3 June 1964, 2 ♂, A. Stauch. 2725, 27 May 1964, juv, 29 ♂ (1 adult), 13 ♀, A. Stauch. 2727, Nov. 1962, 9 ♂, 12 ♀, A. Crosnier. 2728, 26 June 1964, 1 ♂, 1 ♀, A. Stauch. 2729, 27 May 1964, 2 ♂, A. Stauch. 2730, July 1963, 2 ♀, A. Crosnier. 2731, Estuaire de la Songolo, near Pointe-Noire, 1 ♀, A. Stauch.

ANGOLA

2732, off Cabinda, Dec. 1962, 6 ♂, 8 ♀ (1 ov), A. Crosnier.

Supplementary literature records.—Baie de Saint-Jean [19°27′N, 16°22′W], Mauritania; Hann, Gorée, M'bour, and Joal, all S of Dakar, Senegal; Baixos das Galinhas, Ilha de Bissau, Portuguese Guinea; Iles de Los, 1 and 3 mi W and NW Tamara, near Cap Matakong, all near Conakry,

Guinea; Grand Lahou, Ivory Coast (Monod, 1956); Gold Coast shelf (Longhurst, 1958); Fernando Póo (Crosnier, 1964); 7°20′N, 12°39′W, Sierra Leone; lagoon at Abidjan, Ivory Coast; Kribi, Cameroon; Morro Peixe, São Tomé (Forest and Guinot, 1966); Cabinda, Luanda, and Baía do Lobito, Angola (Guinot and Ribeiro, 1962).

CALLINECTES ORNATUS ORDWAY

Figures 6, 18d, 20d, 22d, 25

Callinectes ornatus Ordway, 1863, p. 571 (syntypes: labelled "types," 2 ♀, MCZ 5120, Charleston, South Carolina; 1 ♂, 2 ♀, MCZ 5128, Charleston, South Carolina; ♂ [dry], MCZ 5137, Gonaives, Haiti; ♂, MCZ 5136, Cumaná, Venezuela; those from Tortugas and Bahamas not found).- Smith, 1869, p. 8.- Rathbun, 1896, p. 356 (part), pl. 15; pl. 24, fig. 3; pl. 25, fig. 2; pl. 26, fig. 2; pl. 27, fig. 2.- 1898, p. 596.- 1901, p. 48.- 1930, p. 114 (part), text-figs. 15b, 16a, 17a, 18b, pl. 50.- 1933, p. 48, fig. 40.- Young, 1900, p. 188 (var. of *C. diacanthus*).- Verrill, 1908a, p. 366, text-figs. 22c, 23b; pl. 17, fig. 1; pl. 21, fig. 3.- Boone, 1927, p. 32.- Contreras, 1930, p. 232 (part), fig. 4.- Chace, 1940, p. 33.- 1956, p. 154.- Chace and Hobbs, 1969, p. 132, fig. 37e.- Balss, 1957, p. 1692 (part).- Holthuis, 1959, p. 200.- Guinot-Dumortier, 1960, p. 514, figs. 13a, b.- Williams, 1965, p. 172 (part).- 1966, p. 84, figs. 1A, B, 4A, B.- Taissoun, 1969, p. 69, fig. 25A-D, photo 9.- 1973, p. 22, figs. 4D, 5A, photo 1.

Callinectes diacanthus.- A. Milne Edwards, 1879, p. 225 (var. of *C. diacanthus*).- Young, 1900, p. 186 (part).

Neptunus (Callinectes) diacanthus.- Ortmann, 1894, p. 77 (part; specimens c, k, n_3, West Indies; d, e, Brazil).

Callinectes acutidens.- Boschi, 1964, p. 45, pl. 2, figs. e, f, g; pl. 12, figs. 1, 2.

?*Callinectes humphreyi* Jones, 1968, p. 187.

Description.—Carapace (Figure 6) with lateral pair of frontal teeth prominent but submesial pair small, often almost completely rudimentary. Metagastric area of adults not deeply sculptured, anterior width about 2.8-2.9 times length, posterior width about 1.75 times length. Anterolateral margins broadly arched, teeth exclusive of outer orbital and lateral spine progressively more acuminate laterad; first five teeth with posterior margins longer than anterior margins, shouldered, distinctly separated by narrow-based, rounded notches; last two teeth with margins approximately equal in length, separating notches broad, next to last tooth distinctly more acuminate than spiniform last one. Lateral spine trending forward. Surface of carapace with granulations most prominent on anterior half and on mesobranchial regions, granulations smaller and more closely crowded on meso-metagastric and cardiac regions, nearly smooth along posterolateral and posterior borders.

Chelipeds with smoothly granulated ridges on chelae, carpus almost smooth dorsally, inferior lateral ridge terminating in a low tooth occasionally followed by an inconspicuous eminence. Major chela usually with strong basal tooth on dactyl and, especially in adult males, lower margin of propodal finger often decurved near base.

Male abdomen and telson reaching beyond suture between thoracic sternites IV and V, usually with distal portions recessed below plane of sternum in retracted position; telson slightly longer than broad with somewhat inflated sides; sixth segment of abdomen relatively narrow, sides slightly constricted, not parallel. Mature female abdomen and telson reaching as far forward as in male, telson as broad as long. First gonopods of male (Figures 18d, 20d) reaching almost to suture between thoracic sternites VI and VII, overlapping each other completely near base but diverging distally and tapering to usually lanceolate membranous tip; armed subterminally with short retrogressive spinules quite visible at low magnification, somewhat more numerous and longer distally than proximally with tendency to arrangement in rows near tip on ventral and mesial margin. Gonopores of females (Figure 22d) irregularly ovate with apex on long axis directed anteromesad; aperture of each irregularly and broadly lunate, sloping from surface on mesial side under rounded crenate anterior border and rounded eminence on posterior border.

Size of carapace in mm.—Largest male: length 60, width at base of lateral spines 105, including lateral spines 130. Two largest females: length 58, width at base of lateral spines 84, including lateral spines 107—length 69, width at base of lateral spines 83, including lateral spines 99. These two females demonstrate variability in mature form that is characteristic of all species in the

genus. Summary of selected measurements is given in Tables 1 and 2.

Color.—Adult males with carapace dull olive to dark brown, usually with a large, ill-defined, roundish spot of orange or orange-red on each side posteriorly; lateral spines and anterolateral teeth maroon, light blue or whitish, white tipped. Eyestalks purple. Chelipeds proximally similar to carapace, spotted with blue or soft purple and with spines paler, joints red; inner surface of palm white, but with a large bright red patch bordered with purple; fingers mostly purple, tipped with red. Walking legs bright blue above, with a band of scarlet at each joint and a patch of paler blue or green on posterior and lower side of each article; dactyls red or violet. Swimming legs similar in color, but with red articular bands wider, a patch of orange or yellow on each article; dactyl with proximal blue band separated from distal scarlet band by an orange band. Abdomen light blue posteriorly. Females similar to males except upper surface of chela more violet; fingers with white or fuschia colored teeth.

Many individuals less brilliantly colored, juveniles often dull or plain olive-yellow to greenish above. Some males more melanistic, exhibiting shades of dark brown and purple with accents of yellow and brownish red. Albinistic (or light hued) forms not uncommon (Verrill, 1908a as condensed in Williams, 1966; Taissoun, 1969).

Variation.—A close relative of *C. danae* and *C. similis* (shape of carapace, metagastric area, and reduced submesial frontal teeth), *C. ornatus* is perhaps most often confused with *C. danae* because of their broad sympatric geographic ranges. *Callinectes ornatus* has the most obsolescent submesial frontal teeth of the three species, they being entirely absent in many individuals but developed somewhat in others. Within a single lot of equal-sized specimens both extremes may be seen (USNM 48401, Cuba; 18227, Jamaica) and keys to identification based on this character alone are of limited usefulness. The lateral pair of frontal teeth may have either rounded or quite sharp tips in the same lot of specimens (USNM 48401). Both types of variation in frontal teeth may be seen anywhere in the geographic range.

The anterolateral teeth are more acuminate, forward pointing, and longer than in *C. similis*. Brazilian and some Guianian juveniles in samples have erect anterolaterals, relatively longer for their width, and more cleanly separated than teeth on those from Florida, whereas adult specimens from Brazil (also North Carolina and some from Bermuda and Jamaica) tend to have narrower sharper anterolateral teeth than those from Venezuela, Curaçao, Cuba, and especially Florida. A line of iridescent patches occurs along the bases of anterolateral teeth in some individuals. One specimen from Trinidad (BMNH) has coalesced third and fourth teeth on the right side.

Major chelae may be broad, even on moderate sized juveniles (Florida).

The abdomen of males usually is recessed, but may be flush with the sternum as in immature male *C. similis* and *C. danae*, but is never as broad as in *C. similis*.

First gonopods of males usually extend forward to the anterior one-fourth of thoracic sternite VII, but may reach beyond the suture between thoracic sternites VI and VII among individuals in the same lot. Usually overlapping at the base, at least one specimen was seen in which no gonopod overlap occurred. The lanceolate tip is not always well developed in juveniles, and the membranous extreme tip tends to be longer in Brazilian (and North Carolinian) material than through most of the range.

Distribution.—Bermuda; North and South Carolina through southern Florida; northwestern Yucatán to Estado de São Paulo, Brazil (Figure 25).

Habitat.—Essentially a tropical species found mainly on sandy or muddy bottom from shore to about 75 m, the young have also been collected on shell and sponge bottoms. Occurrence in bays and river mouths (Holthuis, 1959; Rouse, 1970; in addition to collection data presented here), as well as entrapment in fresh water (Brues, 1927), indicate tolerance of a broad range of salinity (recordings of 0-50 ‰ in temperatures ranging from 18° to 31°C); nevertheless, most collections have come from waters of relatively high salinity. Taissoun (1969) reported occurrence in a temperature of 9°C, but this is perhaps a reference to *C. similis* which occurs in colder water.

Spawning.—The spawning season probably extends year round. Museum collections studied include ovigerous females as follows: January, Puerto Rico; April, Guyana, Estado de Rio de Janeiro, Brazil; May, Estado de São Paulo, Brazil;

July, Estado de Rio de Janeiro, Brazil; August, Trinidad, Guyana, Surinam; September, Venezuela, the Guianas; December, St. Thomas, Estado de Rio de Janeiro, Brazil. Taissoun (1969) reported ovigerous females from the Golfo de Venezuela in January and May. Undated collections are recorded from southern Florida, Margarita Island, Venezuela, and Estado de São Paulo, Brazil.

Remarks.—It is difficult to distinguish some juveniles, immature males, and adult females of *C. ornatus* from *C. danae* and *C. similis*. Helpful distinguishing comparisons are the following: males have a narrower abdomen than *C. danae;* mature females have a smaller abdomen than *C. danae;* identification of small- to moderate-sized juveniles is often a matter of judgment based on shape of anterolateral teeth, length of obsolescent submesial frontal teeth, and width of the metagastric area.

Width of the metagastric area approaches that of *C. similis* in some individuals and is a good separating character from *C. danae* for juveniles in regions where no confusion with *C. similis* can occur. Borders of this area are more prominently defined than in *C. similis,* but become indistinct with age; in that condition they approach the smoothness of young *C. similis. Callinectes ornatus* apparently shows less variation than *C. danae.*

Callinectes humphreyi Jones, 1968, was based on an albinistic immature female from Barbados (carapace length 29, total width 60 mm). Though its status must remain an enigma because the type was lost through accident in 1969 (dried specimen destroyed by a bloodhound pup; Jones, pers. commun.) and no illustration was furnished with the description, it was characterized as, "nearest to *C. ornatus,* from which it may be immediately distinguished by its very different coloring . . . . *C. humphreyi* is pure white, except for a band of intense violet-purple on the inner surface of each cheliped, which fades to light red in dried specimens. *C. humphreyi* is also distinguished by its smaller size, the deeper, more conspicuous sinuses between the anterolateral teeth, the relatively longer intramedial area and the distinctly triangular shape of the abdomen." The form was found to be quite common along the southwestern coast of the island where it was usually seen quite near shore at low tide, the white color camouflaging the animals well on the area's sandy bottom. In view of the obvious similarity to *C. ornatus,* endemic occurrence, and coloration falling within the range recognized by Verrill (1908a), it seems likely that this is a color variant of *C. ornatus.*

Williams (1966), in restricting *C. ornatus,* noted that syntypes from Charleston, S.C. were from a locality representing an apparent extreme northern limit of geographic range. At that time no other specimens were known from the Carolinas, although the species is abundant in southern Florida. Other material from northeastern Florida as well as North Carolina is now available. There is little doubt that these northern records still represent peripheral localities, as do those from southwestern Florida between Charlotte Harbor and Tampa Bay. Records for *C. ornatus* in New Jersey (Chace and Hobbs, 1969; Taissoun, 1969) represent *C. similis,* the Carolinian congener of *C. ornatus.* Collections from Bermuda are large, and it was primarily on the basis of these that Verrill (1908b) postulated drift of larvae in oceanic currents as island colonizers for the genus.

Locality data for specimens 30-6 and 30-8 in MNHNP (M. Fontaines) from "Chili" identified as *Neptunus diacanthus* Latr. (identified as *C. ornatus* by Rathbun, 1896) are in error.

Material.—Total: 351 lots,1,260+ specimens.

Specimens listed in Rathbun (1930) from USNM and MCZ (listings from New Jersey, North Carolina, South Carolina, Louisiana, and Texas = *C. similis*).

USNM. 161 lots, 646 specimens, including the following not cited above:

BERMUDA

65644, Hungry Bay, Apr. 1928, 1 ♂, E. Deichmann.

UNITED STATES

North Carolina: 77013, Sea Buoy, Beaufort, 10 Oct. 1935, 1 ♂, 1 ♀, J. S. Gutsell.

Florida: 122995, 28°21.5′N, 80°33.5′W, 4 Apr. 1940, 1 ♂, *Pelican* Stn. 207-1. 122987, shoreline, W side Norris Cut, N end Virginia Key, Miami, 23 Aug. 1966, 1 ♀ (juv), col. unknown. 76989, Coral Gables, no date, 1 ♀, 1 juv, J. F. W. Pearson. 76966, Coral Gables, no date, 1 ♀ (parasitized), J. F. W. Pearson. 122994, Biscayne Bay, 5 Sept. 1938, 5 ♂, 5 ♀, USFWS Launch 58. 113459, Pigeon Key, Monroe Co., 7 Aug. 1965, 6 ♂, 4 ♀ (parasitized), R. B. Manning. 122988, beach area and tidal flats SW

end Bahia Honda Key, Monroe Co., 14 June 1964, 2 ♀ (juv), Foster and Kaill. The following from Key West—45805, no date, 1 ♂, H. Hemphill. 71638, 1934, 1 ♀, H. H. Darby. 76992, no date, 6 ♂, 5 ♀, col. unknown. 76988, front of Biol. Stn., 31 Oct. 1922, 7 juv, USBF, S. and F. 76987, no date, 1 ♂, USBF. 76986, front of Biol. Stn., 25 Nov. 1922, 1 ♀ (juv), USBF, F. and S. 76985, Little Salt Pond Key, 7 Nov. 1922, 1 ♂, 1 ♀, (juv), USBF. 76983, 26 Feb. 1919, 1 ♂, 1 ♀ (juv), USBF, H. and S. 76982, no date, 2 ♂, 1 ♀ (juv), USBF. 76981, Marquesas Keys, no date, 4 ♂, 2 ♀, A. S. Pearse. 122997, Marquesas Keys, 11 Aug. 1931, 8 juv, A. S. Pearse. The following from Dry Tortugas—76976, 5 Aug. 1930, 1 ♀ (juv), W. L. Schmitt. 76977, Long Beach, 7 Aug. 1930, 1 ♂, 1 ♀ (juv), W. L. Schmitt. 76978, Long Key, 25 June 1931, 1 ♂, W. L. Schmitt. 76995, from Long Key to Bush Key, 5 Aug. 1930, 1 ♂, 2 ♀ (1 ov), W. L. Schmitt. 77011, Long Key, 25 June 1931, 1 ♂, 1 juv, W. L. Schmitt. 76997, Long Key, Aug. 1930, 3 ♂, 1 ♀, W. L. Schmitt. 77012, Long Key, 24 June 1932, 3 juv, W. L. Schmitt. 76979, Fort Jefferson moat, 26 June 1931, 1 ♂, 1 ♀ (juvs), A. S. Pearse. 71637, Bush Key, 4 Aug. 1934, 1 ♂, 1 ♀, H. H. Darby. 113009, Charlotte Harbor, 30 July 1964, 4 ♀ (juv), from C. H. Saloman, USFWS, Stn. X-9A. 113010, Charlotte Harbor, 27 Jan. 1964, 1 ♂, 2 ♀ (juv), C. H. Saloman, USFWS, Stn. X-9A. 122989, oyster bed, Cape Haze Marine Lab., Sarasota, 21 July 1965, 1 ♂ (juv), R. Cressey. 113007, Tampa Bay, 9 Oct. 1964, 1 ♂ (juv), from C. H. Saloman, USFWS, Stn. B-13. 113008, Tampa Bay, 16 Sept. 1964, 1 ♀ (juv), from C. H. Saloman, USFWS, Stn. B-13.

Unknown locality "South Atlantic and Gulf Coasts of the United States": 2157, no date, 3 ♂, 2 ♀, col. unknown.

BAHAMAS

88653, Bimini, 13 Nov. 1948, 2 ♀ (juv), A. S. Pearse. 88654, Bimini, Nov. 1948, 1 ♀ (juv), A. S. Pearse. 122990, Clifton Bay, Lyford Cay, Nassau, 14 Aug. 1961, 1 ♂, 2 ♀ (juv), W. L. Schmitt. Uncatalogued, Great Inagua Island just N Matthewtown, 20 Jan. 1968, 1 ♂, Gosner. 76994, no date, 1 ♂, Owen Bryant. 122991, British West Indies, no date, 1 ♂, 1 ♀ (juv), R. Robbins.

CUBA

73306, Bahía de la Habana, 11 May 1937, 2 ♂, 5 ♀, W. L. Schmitt. 76481, Siguanea Bay, 12 Apr. 1937, 1 ♂, (juv), Paul Bartsch. 76485 and 76493, Isla de Pinos, opposite Siguanea I., 11 Apr. 1937, 50 juv, Paul Bartsch, R113 and R114. 76492, Isla de Pinos, opposite Siguanea I., 11 Apr. 1937, 2 ♂, Paul Bartsch, R115 and 116.

JAMAICA

122976, 17°53'N, 77°48'W, 18 May 1965, 2 ♂, 1 ♀, *Oregon* Stn. 5396. 73287, Jamaica or Cienfuegos, Cuba, 4 May 1937, 1 ♀, W. L. Schmitt, Stn. 76.

DOMINICAN REPUBLIC

122996, Bahía de Calderas, 1 ♀ (juv), through I. B. de Calventi and S. Jakowska, 10 July 1967.

PUERTO RICO

73286, San Juan, 27 Apr. 1937, 1 ♂, 1 ♀, W. L. Schmitt. 122999, off Fort San Gerónimo, San Juan, 30 Apr. 1937, 1 ♂, W. L. Schmitt.

VIRGIN ISLANDS

St. Thomas: 2457, no date, 1 ♂ (dry), A. H. Riise. St. Croix: 73288, Christiansted, 7 Apr. 1937, 1 ♀ (juv), W. L. Schmitt, Stn. 31. 73289, same, 9 Apr. 1937, 1 ♂, Stn. 34. 76470, Christiansted Harbor, Dec. 1937, 1 ♀, H. A. Beatty, No. 214. Prickly Pear Island: 122981, Vixen Point, Gorda Sound, 15 Apr. 1956, 2 ♂, Nicholson, Schmitt, and Chace, Stn. 111-56, *Freelance*.

BARBUDA

122982, Oyster Pond Landing, lagoon side, 25 Apr. 1959, 6 ♂, 3 ♀ (immat), W. L. Schmitt, et al., Stn. 92-59. 122980, near Oyster Pond Landing, W shore lagoon, 6 Apr. 1956, 4 ♂, 6 ♀ (immat), Schmitt, Chace, Nicholson, and Jackson, Stn. 85-86, *Freelance*. 122978, 6 Apr. 1956, 1 ♂, Stn. 88-56, *Freelance*.

GUADELOUPE

122977, Pointe à Pitre, between Monroux and Rat Is., 30-31 Mar. 1956, 10 (juv), Chace and Nicholson, Stn. 68-56, *Freelance*.

ST. LUCIA

122979, Marigot Lagoon, shore of bay outside, 21 Mar. 1956, 1 ♂, Schmitt, Chace, Nicholson, and crew, Stn. 38-56, *Freelance*.

BARBADOS

76993, 1918, 1 ♀, Barbados-Antigua Exped.

MEXICO

Yucatán: 12992, ocean beach at Progreso, 400 yd W steamship wharf, 30 Mar. 1936, 1 ♂, M. B.

Trautman. 12993, same, 600 yd W steamship wharf, 8 ♂ (6 juv), 1 ♀ (juv), Trautman, Patton, and Costello.

Quintana Roo: 122984, Bahía de la Ascensión, about ⅓ mi W Allen Pt. light, 13 Apr. 1960, 1 ♂, 3 ♀ (juv), Daiber and Rehder, Stn. 66-60, *Blue Goose*. 122983, Bahía de la Ascensión, shore in front Allen Pt. light, 13 Apr. 1960, 1 ♂, 2 ♀ (1 parasitized), 6 juv, Daiber, Stn. 65-60, *Blue Goose*. 122986, Bahía del Espíritu Santo, N shore, 5 Apr. 1960, 2 ♂, 2 ♀ (juv), Bousfield, Stn. 37-60, *Blue Goose*. 122985, Bahía del Espíritu Santo, N shore near Lawrence Pt., 6 Apr. 1960, 1 ♀ (juv), Rehder, Daiber, and Haynes, Stn. 42-60, *Blue Goose*.

BRITISH HONDURAS

76990, Belize, Sergeants Caye, no date, 2 ♀ (juv), P. W. Shufeldt.

VENEZUELA

101824, Estado Falcón, Bahía de Amuay, Península de Paraguaná, May 1957, 1 ♀, F. A. Aldrich. 122965, SE Trinidad and off Orinoco Delta, 09°55′N, 60°53′W, 26 Aug. 1958, 3 ♀ (1 ov, 1 juv), *Oregon* Stn. 2208. 122966, 09°32′N, 60°24′W, 20 Sept. 1958, 4 ♂, 5 ♀ (3 ov), *Oregon* Stn. 2348.

GUYANA

122970, 08°30′N, 58°56′W, 28 Aug. 1958, 1 ♀, *Oregon* Stn. 2228. 122969, 08°20′N, 58°30′W, 29 Aug. 1958, 4 ♀ (2 ov), *Oregon* Stn. 2234. 122975, 06°54′N, 57°47′W, 25 Mar. 1963, 1 ♂, *Oregon* Stn. 4306.

SURINAM

103177, 06°15′N, 55°54′W, 6 June 1957, 1 ♂, *Coquette* Stn. 182. 103178, 06°22′N, 55°03.5′W, 4 June 1957, 37 juv, *Coquette* Stn. 157. 103179, 06°22′N, 55°06′W, 11 May 1957, 1 ♂, *Coquette* Stn. 1. 103180, 06°23′N, 55°05.5′W, 11 May 1957, 1 ♂, 1 ♀ (juv), *Coquette* Stn. 2. 103181, 06°28′N, 54°57.5′W, 11 May 1957, 1 ♂ (juv), *Coquette* Stn. 20. 122968, 06°26′N, 54°20′W, 15 Sept. 1958, 1 ♂, *Oregon* Stn. 2327. 103454, 07°12′N, 57°22′W, 18 Sept. 1958, 1 ♀ (ov), *Oregon* Stn. 2339. 122967, off the Guianas, 1958, 1 ♀ (ov) *Oregon*.

FRENCH GUIANA

122971, 05°56′N, 52°20′W, 11 Sept. 1958, 1 ♀ (ov), *Oregon* Stn. 2307. 122972, off Cayenne, 05°30′N, 52°10′W, 12 Sept. 1958, 1 ♀ (ov), *Oregon* Stn. 2310.

BRAZIL

122973, off N mouth Amazon R., 02°29′N, 48°58′W, 14 Nov. 1957, 2 ♂, (1 juv), *Oregon* Stn. 2058. 122974, off Ceará, 02°23′S, 40°31′W, 12 Mar. 1963, 1 ♀, *Oregon* Stn. 4250. 72313, Villa Bella, São Sebastião, 18 Sept. 1925, 3 carapaces (dry), W. L. Schmitt. 122998, Barro, Santos, 12 Sept. 1925, 5 ♂, 1 ♀, W. L. Schmitt.

AHF. 13 lots, 26 specimens.

UNITED STATES

Florida: Hillsboro Inlet, Sept. 1943, 1 ♂, 2 ♀, (immat), E. R. T. Hillsboro Inlet, 15 May 1945, 1 ♂, 2 ♀, J. S. Garth, No. 8-45. Pompano Beach, Sept. 1944, 1 ♀ (juv), E. R. J. Hawk Channel, Key Largo North, 7 June 1949, 1 ♀ (juv), Stn. LM32-49. Same, 29-31 May 1949, 3 ♂, 3 ♀ (immat), Stn. LM25, LM-27. Key Largo, Florida Bay, 0.8 km SW "My Place" near Hamper Pt., 23 May 1949, 2 parasitized apparent ♀♀, Stn. LM18-49. Hawk Channel, Plantation Key near Tavernier Creek, 26 May 1949, 1 ♂ (juv), Stn. LM21-49. Lower Matecumbe Key, Hawk Channel, 5.3 km SW Indian Key Drawbridge, 23 Sept. 1950, 1 ♀ (juv), Stn. LM-57. Hawk Channel, Grassy Key, E coast 1.6 km S "Seaside Cabins," 24 May 1949, Stn. LM19-49. Margo Island near channel S Big Marco Pass, 14 June 1949, 1 ♂ (juv), Stn. LM39-49.

CURAÇAO

Schottegat, Santa Anna Harbor, 12°07′03″N, 68°55′34″W, 23 Apr. 1939, 2 ♀, *Velero III* Stn. A47-39.

VENEZUELA

Isla Cubagua, 10°48′48″N, 64°13′30″W, 30 Apr. 1939, 2 ♂, 1 frag., *Velero III* Stn. A30-39. Isla Cubagua, 10°49′25″N, 64°16′W, 15 Apr. 1939, 1 ♀ (juv), *Velero III* Stn. A28-39.

AMNH. 26 lots, 73+ specimens.

BERMUDA

11252, 2 Sept. 1932, 1 ♀ (juv), W. Beebe Bermuda Exped. 11223, 1939, 6 ♂, 2 ♀, (juv), W. Beebe Bermuda Exped. 295, no date, 1 ♂, W. M. Rankin. 11220, 1939, 1 ♂, W. Beebe Bermuda Exped. 11250, 1930, 1 ♀ (juv), W. Beebe Bermuda Exped. 11225, 1929, 1 ♂, W. Beebe Bermuda Exped. 11221, 29 Apr. 1937, 1 ♀, W. Beebe Bermuda Exped.

UNITED STATES

Florida: 6684, Indian River, Nov. 1920, 2 ♂ (juv), Prince. 10367, Lake Worth, July and Aug. 1945, 3 ♂ (1 dry), 1 ♀ (juv), W. G. Van Name and A. H. Verrill.

BAHAMAS

11222, North Bimini, June 1939, 1 ♀ (juv), W. Beebe Bermuda Exped. 11291, Bimini, 5 Sept. 1947, 1 ♀, J. C. Armstrong. 11292, Bimini, 1 ♀ (ov), J. C. Armstrong. 11634, Bimini, 14 June 1953, 1 ♀, W. D. Clarke. 11296, Bimini, 21 Oct. 1947, 3 ♂, 2 ♀, J. C. Armstrong. Nassau and Andros Islands, Mar.-Apr. 1930, 1 ♂ (juv), Bacon-Miner Exped. and International Exped. to Andros I. 10368, Andros I., 1926, 1 quart juv and immat, R. A. Miner.

HAITI

1949-1950, 2 ♂, 2 ♀ (1 juv), A. Curtiss. 11219, Bizoton Reef [NW Port au Prince], 4 Mar. 1927, 2 ♂ (1 juv), W. Beebe Exped.

DOMINICAN REPUBLIC

8641, W shore north half of El Cayo [Barahona Harbor], 7 July 1932, 1 ♂, 1 ♀ (juv), J. C. Armstrong. 9395, southern part La Piedra Prieta Reef, Barahona Harbor, 16 July 1932, 1 ♀ (juv), J. C. Armstrong.

PUERTO RICO

2945, Bahía de Guanica, Ensenada, 14 June 1915, 3 juv, R. W. Miner and H. Mueller. 2999, yard at Miramar, Santurce Barrio, San Juan, 14 July 1914, 1 juv, R. W. Miner and L. Estrada.

ANSP. 3 lots, 8 specimens.

UNITED STATES

4897, Lake Worth Inlet, Fla., no date, 1 ♂ (immat), 4 ♀ (immat), H. A. Pilsbry.

BAHAMAS

3489, New Providence Island, no date, 1 ♂, 1 ♀, H. C. Wood, Jr.

HAITI

5422, Port au Prince, 1950, 1 ♂ (dry), A. Curtis.

BMNH. 11 lots, 18 specimens.

UNITED STATES

Florida: 1966.12.5.558/559, coast of Everglades Park, 1 ♂, 1 ♀, Univ. Miami Inst. Mar. Sci. 61.44, south coast of United States, 2 ♂, 3 juv (dry), vi/9, W. Stimpson.

CARIBBEAN SEA

1955.10.6.98/99, Stn. 28 (44), 1 ♂, 1 ♀ (juv), Oxford Univ. Cayman Exped.

ANTIGUA

1967.4.4.136, 1 ♀ (juv), F. H. Mansell, H. M. S. *Dorsetshire*. 1928.12.1.57, 1 ♂, W. R. Forrest.

BARBADOS

1963.5.16.33, 1 ♀, H. M. S. *Frobisher*, 15 Feb. 1933.

TRINIDAD

1962.12.12.2, Mayaro-Point Radix, Stn. 1125, 1 ♂, D. W. Richardson. Unregistered, San Fernanda, 1 ♀, N. Boutakoff.

GUYANA

1958.11.12.27/28, 07°39′N, 57°44′W to 07°47′N, 57°32′W, 23-24 Apr. 1958, 1 ♂, 1 ♀ (ov), Trawler *Cape St. Mary*.

BRAZIL

50.32, 1 ♀ (dry), vi/6.

MCZ. 32 lots, 106 specimens.

BERMUDA

8377, July 1903, 2 juv, O. Bryant. 8459, Sinky Bay, 30 May 1916, 1 ♂, Bermuda Biol. Stn. 8460, Fairyland Bay in eelgrass, 14 Feb. 1916, 1 ♂, W. J. Crozier. 8890, 1 ♂, recd. from E. L. Mark, 19 Oct. 1920. 8891, Tom Woods Bay, 25 Apr. 1916, 1 ♂, 2 ♀ (juv), E. L. Mark. 8892, Sinky Bay, 11 Apr. 1916, 1 ♂ (immat), E. L. Mark. 9203, Richardsons Inlet, S side St. George Island, June 1936, 5 ♂, 6 ♀ (immat), F. A. Chace, Jr. 9256, Vaughns or Whites Bay, St. Davids Island, 18 June 1936, 4 ♂ (juv), F. A. Chace, Jr. 9447, July 1936, 2 juv, L. H. Kleinholtz.

UNITED STATES

South Carolina: 5210, Charleston, no date, 2 ♀ labelled "Types," col. unknown.

Florida: 8749, 1 ♀ (ov), Maynard. 5130, Key West, no date, 1 ♀, C. E. Faxon. 1134, Tortugas, 1 ♀ (juv), Holder, recd. 8 June 1960. 8748, July 1859, 4 ♂, 2 ♀ (juv), Woodbury. 5131, Tortugas, 3 ♂, 1 ♀, Woodbury, recd. from Smithson. Inst., 13 Feb. 1861. 5206, Fort Jefferson, Tortugas, 3 ♂, part of Ordway's material.

BAHAMAS

9481, N entrance Hawksbill Creek, Grand Bahama Island, 8 Apr. 1936. 1 ♂, W. J. Clench. 11673, Alicetown, North Bimini, May 1941, 1 ♀, R. W. Foster and J. Huntington. 9488, Governors Harbor, Eleuthera Island, 2 May 1936, 1 ♂, W. J. Clench. 9426, Simms, Long Island, 7 July 1936, 1 ♂ (juv), Harvard-Bahama Exped.

MNB. 4 lots, 17 specimens.

BRAZIL

Pernambuco: 331, Praia do Pina, Recife, Sept. 1944, 3 ♀ (juv), col. unknown.

Rio de Janeiro: 49, no other data, 1 ♂. 82, Rio Guanabara, no other data, 2 ♂, 9 ♀ (3 juv). Praia do Fundao, Baía de Guanabara, Dec. 1951, 2 ♂, N. Santos.

MNHNP. 9 lots, 16 specimens.

UNITED STATES

Florida: Tortugas, 4 ♂, from MCZ.

FRENCH GUIANA

Stn. 354, 23 m, mud, 12 Aug. 1957, 2 ♂, 1 ♀, juv, J. Durand, ORSTOM II. Stn. 413, 48 m, dead shells-rocks, 24 July 1958, 1 juv, J. Durand, ORSTOM II. Îles du Salut, July 1957, 2 ♂, 1 ♀, J. Durand, ORSTOM II.

Following are a series of dry specimens with poor or questionable locality data that were also determined by M. J. Rathbun in 1896.

Guadeloupe: 1 ♂, 1 ♀, M. Beaupertuis. Chili: 1 ♂, 30-6, 1 ♀, 30-8, M. Fontaines. Côte de Amérique, 1 ♂, 30-19.

RMNH. 60 lots, 200+ specimens.

UNITED STATES

Florida: Bear Cut, N point Key Biscayne, Miami, 15802, 15 Sept. 1960, juv. 15803, 4 Sept. 1960, juv. 15804, 14 Sept. 1960, juv. 15805, 15 Sept. 1960, juv. 18718, 2-9 Sept. 1963, 1 juv. 23385, 6 Dec. 1964, 1 ♀ (parasitized). 24372, 22 Nov. 1964, juv. 23366, 1 Jan. 1965, juv (parasitized). 23415, 9 Jan. 1965, 1 ♂, juv. 23418, Jan. 1965, 1 ♂, juv. 24371, 1 Jan. 1965, juv. 24373, 10 Jan. 1965, juv. 23430, 9 Jan. 1965, juv (parasitized). 23421, 1 Feb. 1965, 1 ♂ and juv (parasitized), all by J. A. Cabrera and L. B. Holthuis. 23271, 16 Jan. 1965, 2 ♀ (parasitized), L. B. Holthuis. 18717, 1-9 Sept. 1963, 2 ♂, 1 juv, L. B. Holthuis. 23377, Pigeon Key, W Marathon, 30 Jan. 1965, 1 ♂, L. B. Holthuis and J. A. Cabrera. 4920, Tortugas, July 1925, juv, H. Boschma. 15632, Marco Beach S of Marco, 12 Sept. 1960, 1 ♀, beached after hurricane Donna, L. B. Holthuis.

BAHAMAS

2853, Nassau, New Providence, 1887, 2 ♂, 1 ♀, A. de Haas. 1870, Bahama Islands, no date, 1 ♂, 1 ♀, Dr. de Haas.

ST. MARTINS

23457, freshwater pond, 3 Oct. 1963, 2 ♀ (juv), P. W. Hummelinck. 14997, Great Bay, 23 June 1955, 2 juv, P. W. Hummelinck. 11870, Oyster Pond, E coast, 22 Feb. 1957, 4 juv, L. B. Holthuis. 11872, coast near Philipsburg, 16-17 Feb. 1957, 1 ♀, 2 juv, L. B. Holthuis. Simsons Bay, washed ashore on beach, 19 Feb. 1957, 1 carapace (dry), L. B. Holthuis. 11873, freshwater pond W Philipsburg, 17 Feb. 1957, 3 ♂, 1 ♀, 1 juv, L. B. Holthuis. 11875, Simsons Bay, 23 Feb. 1957, 20 juv, L. B. Holthuis.

VENEZUELA

10721, Margarita Island?, possibly Caracus Bay, Curaçao, 1955, 2 ♀ (1 ov), P. W. Hummelinck. 1868, coast, no date, 1 ♂ (juv), T. Buitendijk.

ARUBA

2372, Vaardenbaai (?), 1 June 1905, 1 ♂, Prof. Boeke. Pova Beach, NW coast of island, 27 Apr. 1955, 3 ♂ (dry), J. S. Zaneveld and P. W. Hummelinck. 1307, 1883, 1 ♂, K. Martin. 2261, lagoon, 3 July 1905, 1 ♂ (juv), Prof. Boeke. 1867, June 1883, 1 ♀ (juv), A. J. v. Koolwijk. 1869, July 1883, 1 ♂ (juv), Dr. de Haas.

CURAÇAO

St. Kruis Baai, 7 Oct. 1948, 2 juv, P. W. Hummelinck. 23351, NW part Piscadera Baai, 25 Nov. 1963, 5 juv, P. W. Hummelinck. Piscadera Baai, 16 Mar. 1957, 1 carapace (beached, dry), L. B. Holthuis. 23393, S part Piscadera Baai, 15 Oct 1963, 1 ♀, col. unknown. 11874, Piscadera Baai, fish trap, 11-14 Feb. 1957, 1 ♂, 1 ♀, L. B. Holthuis. 3272, Schottegat, 10 Feb. 1939, 5+ ♂, 2 ♀, H. W. C. Cossee. 2234, reefwater (lagoon), 2 m, 26 July 1905, 1 ♂ (juv), Prof. Boeke.

BONAIRE

NE coast of Cay, 1 Sept. 1948, 2 ♂, P. W. Hummelinck.

GUYANA

22510, 06°54'N, 57°47'W, 25 Mar. 1963, 2 ♂, *Oregon* Stn. 4306.

SURINAM

22518, 06°16'N, 55°56'W, 19 Feb. 1963, 2 ♂, 2 ♀ (juv), *Oregon* Stn. 4171. 21154, off coast between mouths of Suriname and Coppename Rivers, 25-27 Aug. 1964, 1 ♀ (ov), juv, *Coquette*. 11869, 10 mi N mouth of Suriname R., 6-9 May 1957, juv and subadult, *Coquette*. 14999, mouth Suriname R. near Resolutie, 22 Dec. 1942, 1 juv, D. C. Geijskes. 14996, near lightship *Suriname Rivier*, 3 May 1957, 1 juv, *Coquette*. 18672, 20 mi E lightship *Suriname Rivier*, 20 Feb. 1963, 1 ♂, *Coquette*. 11871, 20 mi from coast, NNW mouth Marowijne R., 8-12 Apr. 1957, 1 ♂ (juv), *Coquette*.

FRENCH GUIANA

11868, 06°00'N, 53°29'W, 29 May 1957, 2 ♂, juv, *Coquette*. 14998, 05°56'N, 53°17'W, 21 May 1957, 1 juv, *Coquette*.

BRAZIL

São Paulo: 21587, Ribeira Beach, Ubatuba, 18 July 1962, 1 ♂, L. Forneris. 21694, Enseada Palmas, Anchieta I., Ubatuba, 28 Feb. 1962, 1 ♂ (juv), L. Forneris. 21695, Pedra Andorinha, Ubatuba, 22 Jan. 1963, 1 juv, L. Forneris. 17536, Santos, 12 Sept. 1960, 3 juv, L. R. Tommasi. 17537, Santos, 20 Apr. 1961, 1 ♂ (juv), L. R. Tommasi.

SADZ-B. 27 lots, 125 specimens.

UNITED STATES

Florida: 1466, Key West, 1883, 2 subadult carapaces (dry), Jordan.

BRAZIL

Rio de Janeiro: 1728, Atafona, 1964, 2 ♂, 1 ♀, N. Meneses. 1959, Praia do Forma, Cabo Frio, July 1957, 1 ♂ (juv), Luiz Tommazi. 3255, Praia do Forte, Cabo Frio, Jan. 1964, 1 ♀, S. J. Rand, N. Papanen, S. Tocchetreu, and S. Tacla. 2336, Ilha Grande, Dec. 1965, 1 ♀ (ov), *Emilia* Stn. 14. 3084, Ilha Grande, 30 July 1966, 1 ♀ (ov), *Emilia* Stn. c-288. 2335, Ilha Grande, no date, 1 ♀, Stn. 12. 3226, S side Ilha Grande, 43 m, mud, 17.8°C, 26 Apr. 1968, 2 ♀ (1 ov), Hydrographic Stn. 283. 3247, 25 m, dredge, 11 Nov. 1956, 1 ♂, Corvette *Solimoés* Stn. 99/56. 3249, Ilha Grande, Aug. 1960, 2 ♂, *Emilia* Stn. 1. 3261, 3228, Enseada das Estrêlas, Ilha Grande, 18 July 1966, 27 ♂, 5 ♀, 16 juv, G. Melo. 3237, Enseada das Estrêlas, Ilha Grande, 26 Feb. 1966, 22 ♂, 5 ♀, col. unknown. 2339, Enseada das Estrêlas, Ilha Grande, 26 July 1966, 1 ♂, 1 ♀, G. Melo. 3082, Angra dos Reis, Ilha dos Conqueiros, 21 Apr. 1966, 1 ♂, G. Melo.

São Paulo: 3217, Ubatuba, 1905, 1 ♂, E. Garbe. 3259, Ubatuba, 1905, 1 ♀ (juv), E. Garbe. 1745, Ilha Bela, São Sebastião, Mar. 1962, 1 ♂, 1 ♀ (juv), P. E. Vanzolini. 3227, São Sebastião, 1895 [?], 1 ♀ (juv), H. Britski. 348, Ilha São Sebastião, 1915, 8 ♂, 2 ♀ (1 ov), Bicego. 1740, Praia Grande, São Sebastião, Feb. 1962, 2 ♂ (juv), H. Britski. 2109, Santos, 1959, 1 ♂, 1 ♀, Servico Especial Pesca. 1673, Ilha da Moela [near Santos off Guarujá], 18 May 1962, 3 ♂, 2 ♀ (1 ov), C. Jesús. 1671, Baía do Guarujá, 22 May 1962, 1 ♂, 1 ♀, C. Jesús. Praia Grande, São Vincente, 4 Aug. 1954, 1 ♂, 1 ♀, L. Travassas, E. Dente, and Werner. 2064, unknown locality, July 1959, 2 ♂, 2 ♀, *Emilia* (first trip).

YPM. 5 lots, 25+ specimens

BERMUDA

3850, 1901, 1 ♀ (juv), A. E. Verrill and party. 6397, April 1901, 5 ♂, 4 ♀, A. E. Verrill and party. 6398, 1901, 4 ♂, A. E. Verrill and party. 6392, 1901, 1 ♂, Bermuda Biol. Stn. 6394, 1901, several juv, A. E. Verrill and party.

Supplementary literature records.—Southern Florida (Rouse, 1970); Isla de Pinos, Cuba (Boone, 1927).

CALLINECTES DANAE SMITH

Figures 7, 18e, 20e-f, 22e, 24

Lupa dicantha.- Dana, 1852, p. 272, (type: 1 ♂, dry, USNM 2371, Rio de Janeiro, Brazil).- 1855, pl. 16, fig. 7a-c.

Callinectes diacanthus.- Ordway, 1863, p. 575 [10].- A. Milne Edwards, 1879, p. 226 (var. of *C. diacanthus*).- Young, 1900, p. 186 (part).

?*Neptunus diacanthus*.- Heller, 1868, p. 26.- Doflein, 1899, p. 186 (part, the Colombia and Brazil specimens).

Callinectes Danae Smith, 1869, p. 7 (syntypes: 1 ♂, 1 ♀, MCZ 5143; 1 ♂, 1 ♀, YPM 824, Recife [=Pernambuco, Estado de Pernambuco], Brazil, C. F. Hartt). (Type locality restricted by Rathbun, 1930.)

?*Lupa (Neptunus) diacantha*.- von Martens, 1872,

p. 92, (part, the Rio de Janeiro specimens).
Callinectes danae.- Rathbun, 1896, p. 357, pl. 16; pl. 24, fig. 4; pl. 25, fig. 3; pl. 26, fig. 3; pl. 27, fig. 3.- 1898, p. 596.- 1901, p. 48.- 1930, p. 118 (part), text-figs. 15d, 16d, 17b, 18d, pl. 51.- 1933, p. 49.- Verrill, 1908a, p. 370, fig. 22e (not 22d).- Chace, 1940, p. 33.- Chace and Hobbs, 1969, p. 130, fig. 37b.- Holthuis, 1959, p. 201.- Lemos de Castro, 1962, p. 39, pl. 2, fig. 9.- Williams, 1966, p. 86, fig. 2A-D, 4C, D.- Jones, 1968, p. 187.- Taissoun, 1969, p. 75, fig. 28A-D, photo 10.- 1973, p. 33, figs. 4B, 5D, photo 4.
Callinectes.- Kretz and Bücherl, 1940, p. 173, unnumbered col. pl., figs. 1-22.

Description. — Carapace (Figure 7) bearing four frontal teeth, submesial pair no more than half length of lateral pair. Metagastric area of adults with anterior width about 2-2.5 times length, posterior width about 1.5 times length. Anterolateral margins somewhat arched, teeth exclusive of outer orbital and lateral spine varying from often convex sided with subacute tips at orbital end of row to sharper and more spiniform laterally, each with anterior margin shorter than posterior and separated from contiguous ones by narrow-based rounded notches. Surface of carapace rather evenly and smoothly granulate, except granules more widely spaced on epibranchial region and near anterolateral border, most crowded on gastric, mesobranchial, and cardiac regions; nearly smooth along frontoorbital, posterolateral, and posterior borders.

Chelipeds with granulate ridges, upper surface of carpus bearing slightly developed interrupted ridges trending longitudinally with axis of limb, ridges bearing obsolescent granules often better developed in males than in females, inferior lateral ridge terminating in a strong lateral spine or tooth often followed by a strong eminence. Male abdomen and telson reaching beyond suture between thoracic sternites IV and V; telson triangular, longer than broad with somewhat inflated sides; sixth segment of abdomen with sides nearly straight, diverging proximally, poorly calcified proximally except for variably indurated basal portion often connected to distal part by a narrow central column. Mature female abdomen and telson reaching as far forward as in male, sixth segment shorter than fifth, telson triangular with slightly inflated sides. First gonopods of male (Figures 18e, 20e, f) reaching beyond midpoint of thoracic sternite VI, overlapping each other near base, or adjacent, and tapering to narrow membranous tips usually bent ventrolaterally; armed with scattered but mainly dorsal minute spinules and two to four subterminal sternomesial exceedingly slender elongate spinules. Gonopores of females (Figure 22e) broadly and irregularly ovate with apex on long axis directed anteromesad, aperture of each broadly open mesially, narrowing laterally, and sloping from surface on mesial side under curved and rounded superior border and a rounded prominence on posterolateral border.

Size of carapace in mm.—Largest male: length 58, width at base of lateral spines 104, including lateral spines 139. Largest female: length 48, width at base of lateral spines 84, including lateral spines 108. Summary of selected measurements is given in Tables 1 and 2.

Color.—Live males from Cubatão River near Santos, São Paulo, Brazil: Carapace olive, becoming indigo on edges of lateral spines and outer anterolateral teeth in some individuals, more uniformly olive in others; teeth and spines on chelae white tipped; a white patch in deepest part of depression above third walking leg. Cheliped with upper surface of palm, dactyl, part of carpus, and spined edge of merus indigo to purple, and same color in splashes on inside of fingers, distally on merus and laterally on carpus. Flat outer dorsal surface of palm and upper surface of merus reticulate blue and olive (but many crabs predominantly olive on this part). Walking and swimming legs predominantly china blue to azure blue, grading to greenish and olive in darker parts. Lower edge of chelae grading from purple to china blue or azure individually. Chelipeds with inner face of palm, outer face of palm and fingers, lower face of merus, as well as meri of remaining legs and ventral surface of cephalothorax, white.

Described above is a colorful male which should be called the "purple crab" if *C. sapidus* is called a "blue crab." Some individuals are duller and some have a reticulate pinkish-blue cast on the upper surface of chelipeds.

Color notes by Kretz and Bücherl (1940) and Taissoun (1969) emphasized the distal intense purple coloration of legs and a grayish-blue carapace on adult males.

Variation.—Individual variation of first gonopods outlined by Williams (1966) can be elaborated here. The first gonopods of males vary somewhat in length, being either a little longer or shorter than as described above (long in southern, short in northern parts of the range). Males from Rio de Janeiro, Brazil, southward tend to have first gonopods reaching near or beyond the suture between thoracic sternites V and VI, as do some specimens examined from St. Lucia in the Windward Islands, but some south Brazilian specimens have shorter first gonopods. Males from north of Rio de Janeiro, northeastern South America, and the West Indies tend to have first gonopods reaching from near the middle of thoracic sternite VI to the suture between thoracic sternites VI and VII. The ill defined shortening trend is accentuated in Cuban, Honduran, and a single lot of Floridian material, reaching extreme shortness in the Panamanian region of the Caribbean, especially in USNM lot 43931 in which male gonopods extend only to the suture between thoracic sternites VII and VIII. But in these areas, too, there is enough variation that groupings are hard to define.

The lower margin of the major chela is often decurved opposite the molar complex of the propodus and strongly developed proximal tooth of the dactyl.

Distribution.—Bermuda; southern Florida and eastern side of Yucatán Peninsula to Estado de Santa Catarina, Brazil (Figure 24).

Habitat.—*Callinectes danae* is a common species in Brazil where it occurs from muddy estuaries in mangroves and algae covered broken shell bottoms, to beaches and open ocean depths of 75 m. Specific limits of salinity tolerated are not well documented, but ranges indicated are from fresh to full sea water, and perhaps to hypersaline lagoons.

Kretz and Bücherl (1940) gave no specific designation to species of *Callinectes* studied, but they gave (p. 173) a fairly clear description of the first gonopods of *C. danae,* and their figures, especially 2 and 14, indicate this species. *Callinectes danae* is the most abundant member of the genus along beaches from Santos to Rio de Janeiro where they worked.

Park (1969) found *C. danae* only on or adjacent to the ocean side of islands in Biscayne Bay, usually on wave beaten shores. He reported it absent from the Florida Keys.

Spawning.—The spawning season probably extends year round. Museum collections studied include ovigerous females as follows: January, Surinam; February, Rio de Janeiro; March, Puerto Rico, Haiti, Panama; May, Haiti, Estado de São Paulo, Brazil; June, Estado de São Paulo, Brazil; July, Colombia, Rio de Janeiro; August, Estados de Rio de Janeiro and Santa Catarina, Brazil; November, Curaçao, St. Lucia. Undated collections are from Estados de Bahia, Rio de Janeiro, São Paulo, and Santa Catarina, Brazil. Taissoun (1969) reported an abundance of ovigerous females from May to July in the Golfo de Venezuela, implying an even longer spawning season.

Economic importance.—Literature available does not deal with commercial exploitation of this species except that incidental reports of purchase in markets and capture on fishing vessels imply fairly general usage.

Vendors along roads NW of Santos, Estado de São Paulo, Brazil, near mangrove swamps sell the crabs alive, displaying bunches of a dozen or so each suspended on strings to which the crabs cling by the chelae when they are out of water.

Remarks.—Closest structurally to *C. arcuatus,* its Pacific counterpart (shape of carapace, metagastric region, male first gonopods, and frontal teeth), *C. danae* also shows similarity to *C. marginatus.* The metagastric area is much alike in all three species. In *C. marginatus* the well separated anterolateral teeth trend forward, and the portion of carapace anterior to the epibranchial line is coarsely granulate. In both *C. arcuatus* and *C. danae,* although anterior borders of the anterolateral teeth are shorter than posterior borders, the teeth point outward rather than sweep forward. *Callinectes danae* is quite smoothly granulate over most of the carapace; *C. arcuatus* is much the same but shows more sculptured relief. Among males of the three, *C. marginatus* has much the slenderest abdomen for its length. The telson of *C. danae* males is relatively longer than in *C. arcuatus.*

Width of the sixth abdominal segment in adult female *C. danae* is relatively greater than in adult female *C. ornatus,* a character valued by Rathbun (1930) but one that requires practice to assess. Williams (1966) misnumbered the sixth abdominal segment as the fifth in discussing this character.

Specimens of *C. danae* reported from Chile in literature must be regarded as of uncertain origin, either mistakenly identified with this Atlantic species by early naturalists unfamiliar with similar Pacific forms, or carried from the Atlantic to Pacific sides of South America by sea captains or collectors who recorded destination of voyages as country of origin rather than source of collection (Garth, 1957). Locality data for USNM 20270 (1 ♂), and MNHNP 30.3, 30.2, 30.10, 30.11, 3 [?], S31 (dry, 5 ♂, 1 ♀) listed as "Chili," and 30.20 (1 ♂, dry) as "Amerique" [labelled as *Neptunus diacanthus*], col. Fontaines, are erroneous or incomplete. Corrected identifications were also made by Rathbun in 1896.

A carapace and abdomen of an immature male from the Pleistocene of Maryland (Wailes Bluff: Bed 1) reported as *Callinectes ornatus* by Blake (1953) is probably *C. danae*. Shape of the abdomen is nearer to *C. danae* or *C. similis* than *C. ornatus*, and the metagastric area in both proportions and granulation is most like the average condition for modern *C. danae*, next nearest to *C. sapidus*, and not like *C. ornatus*.

Material.—Total: 202 lots, 782+ specimens.

Specimens listed in Rathbun (1930) from USNM (24427, 24428, 24429, 22044, not found; 20115, 22817 = *C. similis;* 60984 = *C. ornatus;* 1 ♂, 1 ♀ 40591 = *C. marginatus*) and MCZ (4278 not found).

USNM. 86 lots, 310+ specimens, including the following not cited above:

UNITED STATES

Florida: 77087, Long Key, Tortugas, 5 Aug. 1930, 1 ♂ juv, W. Bullington. [?] Uncatalogued, Pompano Beach, Sept. 1943, 1 ♂, E. R. Tinkham.

CUBA

123003, Bahía del a Habana, 11 May 1937, 2 ♂, W. L. Schmitt. 99862, Playa Baracoa, 16 Nov. 1954, 1 ♂ juv, K. K. Caldwell et al. 99916, Playa Baracoa, Fisheries Lab., 16 Nov. 1954, 1 ♀, H. H. Hobbs, Jr. 99937, E Xanadú, Hicacos Pen., Matanzas Prov., 24-27 Jan. 1957, 1 ♂, W. L. Schmitt.

JAMAICA

42854, Montego Bay, 20 July 1910, 1 ♂ juv, C. B. Wilson. 46246, Montego Bay, 12 Nov. 1910, 1 ♂, A. E. Andrews. 61364, 4 Feb. 1928, 2 ♀ juv, C. R. Orcutt.

PUERTO RICO

24421, Palo Seco, Bahía de San Juan, 13 Jan. 1899, juv 2 ♂, 1 ♀, *Fish Hawk*. 123004, Bahía de San Juan, 29 Mar. 1937, 1 ♀, W. L. Schmitt. 73280, Boca de Cangrejos, 7 mi E San Juan, 31 Mar. 1937, 1 ♀ (ov), W. L. Schmitt.

VIRGIN ISLANDS

St. Croix: 77101, Rust-op-Twist, on sea coast, no date, 1 ♂, 2 juv, H. A. Beatty. 72833, St. Croix, Salt River, no date, 8 juv, H. A. Beatty.

ST. LUCIA

22044, Port Castries, 29 Nov. 1887, 5 ♂, 6 ♀, *Albatross*.

MEXICO

Quintana Roo: 123002, Bahía del Espíritu Santo, N shore, 5 Apr. 1960, 1 ♂ (parasitized), E. L. Bousfield.

HONDURAS

78099, Utila I., 25 mi off coast, Sept. 1938, 1 ♂, Louis Mouquin.

PANAMA

59283, 1912, 2 ♂, 2 ♀, 4 juv, Meek and Hildebrand. 59344, no date, 1 ♀, Meek and Hildebrand. 77089, Fox Bay, Colón, 23 Feb. 1935, 2 ♂ juv, S. F. Hildebrand. 89575, Galeta Pt., Ft. Randolph, C. Z., 1949, 2 ♀, 1 juv, V. Walters.

COLOMBIA

105034, Golfo del Darién, 7°56.8′N, 76°47′W to 7°56.5′N, 76°47′W, 8 Feb. 1960, 1 ♀ juv, *Atlantis*.

VENEZUELA

Falcón: 101825, Bahía de Amuay, Península de Paraguaná, May 1957, 1 ♂, F. A. Aldrich. Miranda: 89645, Tacarigua de la Laguna, 1 Mar. 1949, 1 ♂, Soc. Cienc. Nat. La Salle, Stn. C-4. Sucre: Gulf of Paria, 10°29′N, 62°30′W, 24 Oct. 1963, 1 ♂, *Oregon* Stn. 4495. Delta Amacuro: 123001, off Orinoco Delta, 09°39′N, 60°49′W, 26-27 Aug. 1958, 1 ♀, *Oregon* Stn. 2211.

BRAZIL

40590, 1875-77, 1 ♀ juv, Hartt. Rio de Janeiro: 77086, São Francisco, 25 Aug. 1925, 1 ♂, 2 ♀ juv, W. L. Schmitt. 77107, Porto da Inhauma, May 1935, 11 ♂, 12 ♀, Doris Cochran. Paraná: 77095, 77096, Paranaguá, 3 Oct. 1925, 4 ♂, 1 ♀ juv, W. L. Schmitt.

AHF. 3 lots, 3 specimens.

CURAÇAO
Schottegat, Santa Anna Harbor, 23 Apr. 1939, 1 ♂, *Velero III* Stn. A47-39.

TRINIDAD
West Manzanilla, 10°30'N, 61°02'W, 18 Apr. 1939, 1 ♀, *Velero III* Stn. A36-39. Port of Spain, 18 Apr. 1939, 1 ♂, *Velero III* Stn. A37-39.

AMNH. 13 lots, 57 specimens.

HAITI
11219, Bizoton Reef, 4 Mar. 1927, 1 ♀ (ov), W. Beebe Exped. 11224, 21 May 1927, 2 ♀ (ov), W. Beebe. 11242, 1927, 1 ♀, W. Beebe. Unreg. 1949-50, 1 ♂, A. Curtiss.

SANTO DOMINGO
9393, NW corner Bahía de Neiba, Bahía de Barahona, 6 July 1933, 23 juv, J. C. Armstrong. 9394, N half of El Cay, Bahía de Barahona, 7 July 1933, 1 ♂, J. C. Armstrong.

PUERTO RICO
2681, Ensenada, 17 June 1915, 1 ♀, R. W. Miner. 2695, Ensenada, June 1915, 2 ♀, Mayer. 2665, San Juan, Palo Seco Pt., 18 July 1914, 7 ♂, 5 ♀, R. W. Miner. 2899, San Juan, 17 July 1914, 1 ♂, R. W. Miner. 2687, San Juan, 1 Aug. 1914, local boys. 2680, Id. S Catano R. mouth Cano de San Fernando, San Juan, 11 July 1914, 1 ♂, 1 ♀, R. W. Miner and J. T. N..

PANAMA
11241, Bahía de Colón, no date, 4 ♂, 5 ♀, *Arcturus* Exped.

ANSP. 2 lots, 3 specimens.

UNITED STATES
3394, America, no date, 1 ♂, 1 ♀, E. Wilson and I. Lea [listed in catalogue as N. America].

CUBA
4697, Cojímar near La Habana, 10 July 1940, 1 ♂, R. A. McLean.

BMNH. 13 lots, 20 specimens.

BARBADOS
72.28, no date, 2 ♂ juv, F. G. Beckford.

WEST INDIES
43.7, no date, 1 ♀ (dry) vi/9.

TRINIDAD
1962.12.12.1, Tapora Point, 1 ♂, D. W. Richardson, Stn. 1123. Unreg., San Fernando, 2 ♂, N. Boutakoff. 1962, Tapora Point, 9 Feb. 1962, 1 ♂ juv, D. W. Richardson, Stn. 1121/3.

BRAZIL
919b, 2 ♂ (dry) vi/6/7, C. Stewart. 919a, 1 ♂ (dry) vi/7, C. Stewart. Pernambuco: 80.37, juv. 1 ♂, 1 ♀, W. Forbes. Bahia: unreg., 1 ♂ (dry) vi/6. Rio de Janeiro: 1952.3.6.12, 1948, 1 ♂, P. Drach. 74.20, 3 ♀ (2 ov), A. Fry. 50.32, Rio de J. market, 2 ♂, juv (dry) vi/6/7, Rothesay.

MCZ. 10 lots, 102 specimens including the following not cited above.

CUBA
10886, Cienfuegos, 29 Mar.-1 Apr. 1939, 3 ♂, 2 ♀, Harvard-Havana *Atlantis* Exped.

COLOMBIA
5135, Cartagena, no date, 1 ♂ juv, A. Schott.

TRINIDAD
9975, Otheite, 9 mi N La Brea, 22 Aug. 1937, 1 ♂, 1 ♀, 2 juv, E. Deichmann. 9958, Caroni Swamp, 8 Aug. 1937, 1 ♂, 3 ♀, E. Deichmann.

BRAZIL
Rio de Janeiro: 5145, no date, 61 specimens. Thayer Exped. 5146, recd. 1 Dec. 1863, 4 ♂, G. N. Davis. São Paulo: 5142, Santos, no date, 4 ♂, 1 ♀ juv, Coutinho, Thayer Exped.

MNB. 7 lots, 44 specimens.

BRAZIL
Pernambuco: 60, no date, 24 ♂, 5 ♀. Rio de Janeiro: 65, Rio-Guanabara, 2 ♂. Unnumbered, Praia do Fundão, Baia de Guanabara, Dec. 1951, 1 ♂, N. Santos. 51, Rio-Guanabara, 5 ♂, 3 ♀. 260, Recreio dos Bandeirantes-Guanabara, 24 May 1953, 1 ♂, N. Santos. São Paulo: 54, Santos, 1 ♀ (ov). Santa Catarina: 53, São Francisco do Sul, no date, 1 ♂, 1 ♀, L. Jualberti.

MNHNP. 3 lots, 6 specimens.

BRITISH HONDURAS
Belize, 1 ♂ (dry), date, col. unknown.

BRAZIL

30-21, 1 ♂ (dry), date, col. unknown. Santa Catarina, 1875, 1 ♂, 1 ♀ (ov), Vignes 1129. 202.64, Desterro [= Florianópolis], 1 ♂ (dry), M. Müller.

ARGENTINA [?]

Suitreé [?], 1922, 3 ♂ (dry), from Museo de Historia, Nat., Buenos Aires. Incomplete data or erroneous localities: 6 ♂, 1 ♀ (dry) from "Chile" and "Amerique" by M. Fontaines and col. unknown. (No. 30.3, 30.2, 30.10, 30.11, 30 [?], 30.20, and S31).

RMNH. 21 lots, 49+ specimens.

ST. MARTIN

Great Bay, 7 June 1955, 1 ♂, P. W. Hummelinck. 10716, freshwater pond, 27 July 1955, 1 ♀, P. W. Hummelinck. 11850 and 1112, freshwater pond W Philipsburg, 17 Feb. 1957, 2 ♀, juv, L. B. Holthuis.

MARTINIQUE

3273, Fort de France, 6 Feb. 1939, 1 ♀, H. W. C. Cossee.

PANAMA

Canal Zone, Bahía de Limón, N Limón Point, 5 July 1966, 6 juv, *Pillsbury* Stn. 322.

COLOMBIA

23518, Golfo de Urabá, 08°0.1′N, 76°50.3′W to 08°1.2′N, 76°47.7′W, 12 July 1966, 3 ♂, 2 ♀ (1 ov), 2 juv, *Pillsbury* Stn. 357.

NETHERLANDS ANTILLES

Aruba: 15040, Lagoon NW Savaneta, 21 Mar. 1957, 2 juv, L. B. Holthuis.

Curaçao: St. Kruis Baai, 7 Oct. 1940, 1 carapace, P. W. Hummelinck. 15038, within St. Martha Baai, near St. Nicolaas, 3 Nov. 1957, 1 juv, L. B. Holthuis. 11852, Piscadera Baai, 11 Feb. 1957, 2 ♂, 1 ♀, L. B. Holthuis. 15039, Piscadera Baai, mudflat behind mangroves, Caraibisch Mar. Biol. Inst., 24 Jan. 1957, 1 ♀ juv, L. B. Holthuis. 10717, Caracas Baai, Nov. 1954, 1 ♀ (ov), J. S. Zaneveld. 11849, Waaigat, Willemstad, 30 Jan. 1957, 3 ♂, 3 ♀, L. B. Holthuis. 11851, South shore St. Joris Baai at Choloma, 3 Jan. 1957, 3 ♂, 1 ♀, L. B. Holthuis.

TRINIDAD

23368, and unnumbered, Diego Martin River, 1965-66, 2 ♂, H. O. von Hagen.

SURINAM

11848, near lightship *Suriname Rivier,* 12-13 Jan. 1953, 1 ♀ (ov), H. W. Lijding.

BRAZIL

Cat. a, no date, 2 ♂ (dry). 375, Bahia, 1909, 5 juv ♂ and ♀, J. A. Bierens de Haan.

ATLANTIC OCEAN

1859, 1 ♂ juv, R. Conradsen.

SADZ-B. 43 lots, 186+ specimens.

BRAZIL

Bahia: 2098, Ilha de Itaparica, July 1959, 1 ♂, Tagea Bjornberg. 350, June 1896, 1 ♂, 1 ♀, Bicego. 3225, Ilhéus, 1919, 4 ♂, 1 ♀, E. Garbe. 1725, Ilha Madre de Deus, 1932, 1 ♂, Oliviera Pinto. Rio de Janeiro: 401, São João da Barra, 1911, 2 ♂, E. Garbe. 3239, Atafona, 12 July 1963, 5 ♂, 6 ♀, N. Meneses. 3213, Atafona, lagoon, 3 ♂, 6 ♀, N. Meneses. 1730, S. J. Barra, 1963, 1 ♂, N. Meneses. 3232, Macaé, 24 Oct. 1942, 1 ♂, A. Castro and J. Feio. 370, Rio de Janeiro, 1898, 1 ♂, Bicego. 3252, Ilha Grande, 17 May 1966, 1 ♀ juv. 3256, Angra dos Reis, 27 July 1966, juv. 3257, Praia do Baia, Angra dos Reis, 20 May 1966, 1 ♀, G. Melo. 3258, Praia Grande, Angra dos Reis, 18 May 1966, 1 ♂, G. Melo. 1734, Angra dos Reis, 1945, 1 ♂, 1 ♀, 1 juv, L. T. Filho. 3083, Ilha Grande, 14 May 1966, 1 ♀, *Emilia.* 3238, Enseada das Estrêlas, Ilha Grande, 26 Feb. 1966, 13 ♂, 10 ♀ (2 ov). 3260 and 3229, Enseada das Estrêlas, Ilha Grande, 18 July 1966, 26 ♂, 24 ♀ (8 ov), G. Melo. 3248, [off Rio de J.?], 11 Nov. 1956, 1 ♂, Corvette *Solimoés,* Stn. 99/56.

São Paulo: 891, São Sebastião, 1915, 3 ♂, 4 ♀, E. Garbe. 1724, São Sebastião, no date, 2 ♂, 2 ♀, P. E. Vanzolini. 1741, Praia Grande, São Sebastião, Feb. 1962, 1 ♀, H. Britski. 2108, São Sebastião, July 1959, 2 ♂, H. R. Costa. 1737, 3253, Estrada Caraquatatoba, São Sebastião, no date, 1 ♂, 2 ♀, 1 carapace. 3251, Farol da Moela, Aug. 1965, 1 ♀, Inst. Pesca Santos. 1662, Farol da Moela, Mar. 1964, 4 ♀ (1 ov), Inst. Pesca Santos. 522, Piassaquera, Jan. 1914, large left merus of chela. 398, Piassaquera, Sept. 1910, 3 ♂, 3 ♀. 359, Piassaquera, June 1903, 5 ♀ (2 ov), Luederwaldt. 1813, Santos, 11 Sept. 1962, 2 ♂, 6 ♀, G. Melo. 1732, Santos, no date, 2 ♀, E. Rabello. 1735, Porto Nôvo, Santos, Nov. 1947, 2 ♂, L. Damico. 1403, Itanhaen, May 1926, 1 ♂, R. Spitz. 1407, Itanhaen, May 1927, 1 ♂, 1 ♀ (ov), R. Spitz. 1302, Itanhaen, July 1935, 1

♀, R. Spitz. 3236, Praia da Trincheira, Cananéia, 27 June 1964, 6 ♂, Cory and Isauro.

Santa Catarina: 665, Itajá, 1900, 3 ♂, Luederwaldt. 3235, Praia de Itapema, Itapema, July 1965, 1 ♂, Dep. Zool. Exped. 3244, 27°15′S, 48°47′W, 70-75 m, sand-shell, 21 Aug. 1966, 3 ♂, 2 ♀ (1 ov), M. Iwai. Rio Grande do Sul: 3233, Praia de Torres, 5 Oct. 1964, 2 ♂, J. Bertoletti. 3250, Praia na desembocadure, Rio Tramandai, 8 Apr. 1965, 2 ♂ juv, R. P. Leal.

YPM. 1 lot, 2 specimens.

BRAZIL

824, Pernambuco, 1867, 1 ♂, 1 ♀, C. F. Hartt.

Supplementary literature records.–Bermuda (Verrill, 1908a); Florida (Futch, 1965; Park, 1969); Golfo de Venezuela and Estr. de Maracaibo, Venezuela (Taissoun, 1969); Curaçao (Nobili, 1897); Barbados (Jones, 1968); Barra das Jangadas [S Recife], and estuaries, Pernambuco, Brazil (Coêlho, 1966, 1970, 1971); Ilha de São Sebastião and ocean beaches, Estado de São Paulo, Brazil (Luederwaldt, 1929; Lavallard, 1960).

CALLINECTES ARCUATUS ORDWAY

Figures 8, 18f, 20g-h, 22f, 24

Callinectes arcuatus Ordway, 1863, p. 578 [13] (type: ♂, USNM 61833, Cape San Lucas [Baja California]).- A. Milne Edwards, 1879, p. 228 (var. of *C. diacanthus*).- Rathbun, 1896, p. 362, pl. 20; pl. 23, , fig. 1; pl. 24, fig. 8; pl. 25, fig. 7; pl. 26, fig. 7; pl. 27, fig. 7.- 1898, p. 596.- 1910, p. 537, 577, pl. 56.- 1930, p. 121, text-figs. 15h, 16h, 17f, 18g, pl. 52.- Young, 1900, p. 190 (var. of *C. diacanthus*).- Nobili, 1901, p. 31.- Boone, 1929, p. 564, text-fig. 3.- Contreras, 1930, p. 233, text-fig. 5.- Garth, 1948, p. 35.- 1957, p. 36.- 1961b, p. 141.- Garth and Stephenson, 1966, p. 43, pl. 5, fig. A; pl. 8, fig. A; pl. 10, fig. A; pl. 12, fig. D.- Buitendijk, 1950, p. 275.- Bott, 1955, p. 56.

Callinectes pleuriticus Ordway, 1863, p. 578 [14] (syntypes: 2 ♂, 1 ♀, MCZ 4701; ♂, MCZ 987; Panama, A. Agassiz).- A. Milne Edwards, 1879, p. 228 (var. of *C. diacanthus*).- Young, 1900, p. 190 (var. of *C. diacanthus*).

Callinectes sp. Smith, 1871, p. 91.- Lockington, 1876, p. 107 [13].

?*Neptunus diacanthus* Brocchi, 1875, p. 54, pl. 16, fig. 82.- Cano, 1889, p. 90, 99, 100, 102, 211.- Doflein, 1899, pl. 186 (part; the Ecuador specimen).

Callinectes nitidus A. Milne Edwards, 1879, p. 228, explan. pl. 41 (var. of *C. diacanthus*) (syntype: ♂, USNM 20269, Tanesco [= Tahuesco, 14°01′13″N, 91°07′03″W] Guatemala, on the borders of the Esteros).- Young, 1900, p. 190 (var. of *C. diacanthus*).

Callinectes diacanthus.– A. Milne Edwards, 1879, pl. 41 [var. *nitidus*].

Callinectes dubia Kingsley, 1879, p. 156 (type: ♂, MCZ 5178, Gulf of Fonseca, west coast of Nicaragua, J. A. McNeil).- Young, 1900, p. 191.

?*Neptunus (Callinectes) diacanthus* Ortmann, 1894, p. 77 (part; the S. Chile specimen).

Callinectes diacanthus.- Young, 1900, p. 186 (part).

Description.—Inflated carapace (Figure 8) bearing four triangular frontal teeth, submesial pair no more than half length of lateral pair. Metagastric area of adults with anterior width about 2.5 times length, posterior width between 1.3 and 1.5 times length. Anterolateral margins arched, teeth exclusive of outer orbital and lateral spine well separated and varying from convex–sided with subacute tips at orbital end of row to sharper and more spiniform laterally, each with anterior margin shorter than posterior. Surface of carapace with granulation fairly uniform, most crowded on gastric, mesobranchial, and cardiac regions, more scattered near anterolateral margins, and smooth along frontoorbital, posterolateral, and posterior borders. Epibranchial line prominent, interrupted slightly at corner of mesogastric area.

Chelipeds with sharply granulate ridges on propodus, basal portion of dactyl, and exposed surfaces of carpus. Dactyl of major chela with large basal tooth closing against molariform complex at base of propodal finger, lower margin of propodal finger often decurved near base in adults.

Male abdomen and telson reaching beyond suture between thoracic sternites IV and V; telson triangular, longer than broad; sixth segment of abdomen with sides nearly straight distally, diverging proximally, segment poorly calcified proximally except for triangular basal portion connected to distal half by a narrow (sometimes obsolescent) central indurated column. Mature female abdomen and telson reaching as far forward as in

male, last two segments nearly equal in length, telson triangular with slightly inflated sides, apices acute. First gonopods of male (Figures 18f, 20g, h) reaching about to abdominal locking tubercles on fifth sternite, often partially overlapping near base, tapering to narrowly flared tips bent ventrolaterally and opening mesioventrally, armed with scattered minute spinules sternally and laterally and with a subterminal sternomesial row of elongate slender spinules. Gonopores of females (Figure 22f) elliptical with long axis in transverse plane, sinuous aperture of each with rounded margins except mesial side sloping from surface under overhanging anterior and inferior bulbous posterolateral border.

Size of carapace in mm.—Largest male: length 54, width at base of lateral spines 93, including lateral spines 123. Largest female: length 55, width at base of lateral spines 96, including lateral spines 114. Summary of selected measurements is given in Tables 1 and 2. Estévez (1972) judged females to attain sexual maturity at a length of 28-34 mm, but smaller ones are known (see Spawning).

Color.—Male: "Carapace dull olive gray-green. Chelipeds olive green dorsally, whitish ventrally, washed with bluish-violet and chelae tipped with pale yellow-brown. Legs turquoise washed with olive; hairs straw gold; swimming legs olive green with suggestion of turquoise, paddles washed with black; hairs straw; tubercles at leg joints golden orange; eyes straw with brownish streaks; underparts pure white" (Garth, 1961b; Garth and Stephenson, 1966).

Female: Carapace generally blue, central portion blue violet; anterolateral portions deep purplish-vinaceous. Chelipeds with base of merus olive, inner portion of hands blue-violet, remainder purplish but varied, fingers barred with purple, propodal fingers usually white tipped. Remaining legs Italian blue, hairs olive, swimming legs with articulations and margins narrowly violet, paddles sometimes turquoise. Abdomen violet, joints and sternum white (Garth, 1961b).

Variations.—Lateral spines in *C. arcuatus* vary considerably, some being relatively no longer than in *C. exasperatus*. Inner orbital fissures are open in some individuals. Chelipeds often have smooth ridges rather than granulate ones, and the propodal molariform complex of the major chela is often worn. The proximal portion of abdominal segment 6 may be almost completely uncalcified in males.

Variations in *C. arcuatus* are often those associated with proportional growth changes. These are pronounced enough to make identification difficult, especially among juveniles. *Callinectes pleuriticus* and *C. dubia* were based on immature *C. arcuatus*. The mesogastric area grows relatively broader with the maturing carapace. Adult females have a more arched carapace than the immature, and seemingly more females than males have a hairy growth under the anterolateral border. First gonopods of juvenile males are short; those of adult males range in length from short, with tips terminating at level of the suture between thoracic sternites VI and VII, to long, terminating near the suture between thoracic sternites IV and V. The tips of these appendages usually curve ventrolaterally but may curve ventrally, mesially, or asymmetrically, and the slender distal portions occasionally are sinuous rather than straight. Subterminal dorsal spinules may be worn off of first gonopods.

An ovigerous female from Panama (AHF, Stn. 111-33) has seven anterolateral teeth on the left side.

Distribution.—Los Angeles Harbor, Calif., to Mollenda, Peru; Galápagos Islands (Figure 24). The record from southern Peru is an immature male. A record from the Galápagos Islands in April 1941, is a soft mature male, and two other records in February 1964, are an immature male and female.

Habitat.—Garth and Stephenson (1966) summarized habitat as sand or mud bottom, oyster beds, lagoons, estuaries, channels among mangroves, or river mouths. Recorded depth range is shoreline to 27.5 m, with many occurrences limited to shallows less than 1 or 2 m along shore, but Estévez (1972) reported common occurrence in Colombia on sand or sand-mud bottom, preferentially between 10 and 20 m in salinities 22‰ or higher. Estévez found the diet included mainly crustaceans, bivalves, fishes, inorganic remains, gastropods, and cephalopods in order of precedence (330 stomachs examined).

Spawning.—The spawning season extends year round. Museum records include ovigerous females as follows: January, Costa Rica; March, Oaxaca,

Mexico, Panama; April, between San Felipe and mouth of Colorado River, Mexico, Peru; May and June, Sinaloa, Mexico; July, Panama; August, Jalisco, Mexico; September, Guerrero, Mexico; November, Sonora and Jalisco, Mexico; December, Sonora, Mexico. A female from near the mouth of the Colorado River (AHF, Golfo de California, 6-9 April 1947, Stn. H47-53) is the smallest egg bearer seen in this species, the carapace having a length of 23, and width at base of lateral spines 39, or including lateral spines of 52 mm. Month of collection is unknown for an ovigerous female from Anaheim Slough, Calif., in 1928. Estévez (1972) considered ovigerous females rare.

Remarks.—The cognate species *C. arcuatus* and *C. danae* are so similar that differentiation is difficult except on grounds of male first gonopod morphology or geographic distribution. In general, *C. arcuatus* is the more robust species, having a tumid carapace emphasized in the arched anterolateral border and inflated branchial regions. Anterolateral teeth stand up from the surface, as if each is reinforced with an axial rib extending from the borders of the anterolateral area, but almost never are shoulders developed on their margins, whereas in *C. danae* there is less prominent central reinforcement in the teeth but a tendency to development of shoulders. Such differences are inconsistent.

Distribution of *C. arcuatus* along the Pacific side of Baja California parallels, but is more extensive than, that of *C. bellicosus*. In this region, marine climate that is transitional between tropical and dominant temperate extends from Punta Entrada (Bahía Magdalena) to Point Conception north of Santa Barbara Channel (Garth, 1961a). Here temperate and tropical faunas mingle, but tropical elements thin out in the north surviving only in protected areas or in favorable years. Records of *C. arcuatus* along this outer coast are less numerous than in the Golfo de California and southward, but occurrence of an ovigerous female at Anaheim Slough, Calif., indicates enough tolerance of temperate conditions to develop breeding populations, at least in favorable years. *Callinectes arcuatus* shows adaptation to a broader spectrum of marine climates than *C. bellicosus* in its much more extensive distribution from temperate southern California, through the essentially insular oceanic province at the tip of Baja California and tropical eastern Pacific, to temperate fringes of the Humboldt Current along Peru.

Callinectes arcuatus is questionably listed from the Caribbean side of Colombia at Turbo on the Golfo de Urabá in MCZ lot 9666. I agree with the cataloger that this must be an erroneous locality for the collection.

A collection of *C. arcuatus* from Estero de los Algodones, SE of Guaymas, Sonora, Mexico (USNM 15431) contains a large female which has a broken male first gonopod inserted in the left genital opening. The gonopod fragment is 14 mm long, completely inserted, and is that of a male *C. arcuatus*.

Brocchi's (1875) discussion of male gonopods in *Callinectes* is a puzzle because there is no sure way to know which species he studied; neither his descriptions nor figures are accurate enough to allow certainty in forming synonymy. This would be of no real concern were it not for the relationship of his work to that of Milne Edwards (1879). Brocchi studied material obtained from Milne Edwards, and both considered gonopod structure of males to be among the diagnostic characters for species or "varieties" of *Callinectes*. Reasonable assessment of Brocchi's material rests on the geographic source of material then available, his discussion, and its probable influence on Milne Edwards's thinking. The evidence is present in both papers. Summarizing: species with short first gonopods came from the Antilles, coast of America, and Chile; those with long ones came from Cayenne and Guatemala. Chile must be regarded as an erroneous locality for species in this genus (Garth, 1957).

Milne Edwards (1879) described *C. cayennensis* (= *C. bocourti*) with long first gonopods from Cayenne and remarked on likeness of the male gonopods to those of *C. hastatus*. Brocchi (1875) may have worked with *C. bocourti* from Cayenne but more likely with *C. hastatus* (= *C. sapidus*) itself, for he remarked on its broad, strong frontal teeth and designated it as the *hastata* of Ordway (plate 16, Figure 81).

By designation "very long," Brocchi indicated that his illustration of male first gonopods from Guatemalan material (plate 16, Figure 82) must refer to *C. arcuatus*, a species regarded as having nearly straight gonopods (Milne Edwards, 1879).

Species with short male first gonopods from provenances listed by Brocchi (1875) and described in more detail by Milne Edwards (1879) were: Antilles, *C. ornatus* and *larvatus* (= *C.*

marginatus); coast of America, the same species; Chile, species undetermined by either Brocchi or Milne Edwards because of fragmentary information. Brocchi's illustration of a strongly curved gonopod (plate 16, Figure 76) seems closest to *C. marginatus*. Figure 78 depicting a short and straight gonopod seems closest to *C. ornatus* as does the undesignated Figure 79. Figure 77, though clearly called "short," resembles that of *C. bellicosus* in sinuosity. Milne Edwards (1879), making no mention of "long" or "short" gonopods for this species, was impressed with the double curvature, but listed *C. bellicosus* only from Cabo de San Lucas, Baja California. We must regard Figure 77 as possibly an illustration of *C. marginatus* because it seems closest to that species from geographic origins listed.

Following is an outline summary of first gonopod characters as understood by Milne Edwards (1879).

ATLANTIC

hastatus [= *sapidus*]: long, reaching to near end of abdomen; Nantucket to Mobile, perhaps on coast of Brazil.

ornatus: short and straight; Charleston-Cumaná, including Tortugas, Bahamas, also Santa Catarina, Brazil.

larvatus [= *marginatus*]: very short and curved; coast of Florida, Key West, Tortugas, Bahamas, Haiti, Veracruz, Mexico.

tumidus [= *exasperatus*]: long but moderate and distinctly hooked, approaches *hastatus;* Key West, Fla., Haiti.

bocourti: long, to end of abdomen as in *hastatus;* Honduras.

cayennensis [= *bocourti*]: long and reach end of abdomen as in *hastatus;* Guyana.

danae: long and straight; Rio de Janeiro *(diacanthus).*

PACIFIC

toxotes: very long, end of abdomen; Cabo de San Lucas.

robustus [= *toxotes*]: very long as above; Colombia.

bellicosus: "the verges reach almost the middle of the penultimate article, they are incurved strongly and outward near the extremity, then inward similarly and finally the point is directed externally" [sinuous]. Golfo de California; Cabo de San Lucas.

arcuatus: long and straight, resembles *diacanthus* of Rio de Janeiro; but more slender; Cabo de San Lucas.

pleuriticus [= *arcuatus*]: long and straight; Panama.

nitidus [= *arcuatus*]: slender, straight and long; Guatemala, Tanesco.

In addition, those from Chile resemble the Guatemalan forms.

Material.—Total: 199 lots, 655 specimens.

Specimens listed in Rathbun (1930) from USNM [correction, USNM 62050=62051] and MCZ; Garth and Stephenson (1966) from AHF and USNM.

USNM. 76 lots, 316 specimens, including the following not cited above:

MEXICO

Baja California: 64119, Isla San Lucas, 15 Jan. 1930, 1 ♂ juv, M. Valerio. Sonora: 111769, Golfo de Calif.? no date, 1 ♂, T. H. Bullock, Stn. W53-289.

Nayarit: 123089, Estero de San Blas, 7.5 mi by road NNE San Blas, 14 Feb. 1955, juv 6 ♂, 2 ♀, Miller and Greenbank, M55-18. 123090, slough at N end Laguna de Mexaltitán, 28 Mar. 1955, 1 ♂ juv, Miller and Greenbank, M55-74.

GUATEMALA

20269, Tanesco [= Tahuesco, 14°01′13″N, 91°07′33″W] on the borders of the Esteros, 1 ♂ (dry). 123088, Iztapa, 5 Apr. 1950, 1 ♂.

NICARAGUA

77085, El Realejo, no date, 1 ♂ juv, Kingsley.

COSTA RICA

61034, Puntarenas, Mar. 1927, 1 ♂ (dry), M. Valerio. 76137, San Lucas [= Isla San Lucas], 15 Feb. 1931, 2 juv, M. Valerio. 76685, Golfo Dulce, 2 Feb. 1933, 1 ♀ (dry), M. Valerio.

PANAMA

77090, Balboa, C.Z., 4 Feb. 1937, 1 ♂ juv, 1 ♀, S. F. Hildebrand. 77094, Drydock, Balboa, C.Z., 8 Feb. 1937, 1 ♂, S. F. Hildebrand. 76917, Miraflores Locks, C. Z., no date, 2 juv, S. F. Hildebrand. 77081, Farfán Beach, C. Z., 23 Feb. 1937, 1 ♂ juv, S. F. Hildebrand. 77082, Venado Beach, 26 Feb. 1937, 1 ♂ juv, S. F. Hildebrand. 77083, Puerto Pilón, 2 Mar. 1937, 1 ♀ juv, S. F. Hildebrand. 77093, Taboga I., 8 Feb. 1937, 1 juv, H. C. Clark. 82134, Miraflores Locks (Lower Chamber), 4 juv,

S. F. Hildebrand. 82135, Dry Dock, Balboa, C.Z., 18 Mar. 1937, 1 ♂ juv, S. F. Hildebrand. 82136, Miraflores Locks (Lower Chamber), C.Z., 26 and 29 Mar. 1937, 1 juv, S. F. Hildebrand. 111779, Río Antón, Golfo de Panamá, 2 Apr. 1957, 2 ♂, W. L. Klawe. 119846, Punta Paitilla, 24 Feb. 1964, 1 ♂, R. Dutary. 123091, Bahía Piñas, near mouth of estuary at Santa Dorotea, 07°34.5′N, 78°11.5′W, 9 Sept. 1961, 7 juv, *Argosy* Stn. 10. 123092, Bahía Piñas, shallow end along crescent beach to E end at Santa Dorotea, 9 Sept. 1961, 3 juv, *Argosy* Stn. 9.

COLOMBIA

68552, Tumaco, no date, 2 ♂.

ECUADOR

123093, Esmeraldas, in harbor and fish market, 0°57.5′N, 79°42.5′W, 25 Sept. 1961, 1 ♂, *Argosy* Stn. 41. 70990, Salada, Guayaquil, 1 and 2 Oct. 1926, 1 ♂, W. L. Schmitt. 97899, Manta, Prov. Manabí, 0°56′30″S, 80°44′W, Aug. 1949, 1 ♂ (dry), T. Mena. 97930, supra cit., 1 ♀ (dry).

PERU

76574, Paita, 8 Oct. 1926, 1 ♂, W. L. Schmitt. Uncatalogued, Negritos, Apr. 1941, 1 ♂, 1 ♀, H. E. and D. L. Frizzell (160/433).

GALAPAGOS ISLANDS

111676, Conway Bay, 15 Apr. 1941, 1 ♂, W. L. Schmitt.

AHF. 66 lots, 221 specimens, including the following not cited above:

MEXICO

Sonora: Guaymas, tidal flats N of Motel Tular, 22 June 1966, 2 ♂, 1 ♀, R. Reimer and A. Alvarez, Stn. 2a.

Sinaloa: Topolobampo, 25 June 1966, 1 ♂, 1 ♀, R. Reimer and A. Alvarez, Stn. 4g.

Jalisco: Bahía Chamela, North Lagoon, 17 Nov. 1937, 1 ♂, 3 ♀ (2 ov), *Zaca* No. 37,142.

Guerrero: Acapulco Beach, 26-28 Nov. 1937, 1 ♀, *Zaca*-NYZS 37,277.

EL SALVADOR

Golfo de Fonseca, La Unión, 27 Dec. 1937, 1 ♀, *Zaca* Stn. 199, D-8 to D-16, 5-6 fm.

HONDURAS

Golfo de Fonseca, Cutuco and Potosí Lights, 20 Dec. 1937, 4 ♂, 6 ♀, 3 juv, *Zaca* No. 37,666.

NICARAGUA

Corinto, 29 Dec. 1937, 1 juv, *Zaca* Stn. 200, D-7, 3.6 m. Corinto, Castenones Lagoon and mid-harbor, 6 Jan. 1938, 4 ♂, 4 ♀, *Zaca* NYZS 3814. Corinto, 7 Jan. 1938, juv 1 ♂, 1 ♀, *Zaca* 200, D-20 to D-26, 2.7-11.9 m.

COSTA RICA

Port Parker [= Golfo Elena], 13 Jan. 1938, 1 ♂, 3 ♀ (1 ov), 4 juv, *Zaca* No. 3859. Golfo Elena, 22 Jan. 1938, 2 ♂ juv, *Zaca* Stn. 203, D-9, 2.7-7.3 m. Puerto Culebra, 26 Jan. 1938, 8 ♂, 3 ♀, 2 juv, *Zaca* NYZS 38,115. Mata de Limón, 30 July 1964, 2 ♂, J. Mohr. Piedra Blanca [= Bahía Carrillo], 6 Feb. 1938, 2 ♂, 2 ♀, *Zaca* No. 38,195. Golfo de Nicoya, Isla Cedro, 12 Feb. 1938, 1 ♂, *Zaca* NYZS 38,302. Golfo Dulce, Golfito, 5 Mar. 1938, 1 ♂, 1 ♀, 4 juv, *Zaca* No. 38,472. Golfo Dulce, Golfito, 9 Mar. 1938, 1 ♀ juv, *Zaca* 218, NYZS 38,596. Supra cit., juv 1 ♂, 5 ♀, *Zaca* 218, D-4, D-5, D-8, 11 m.

PANAMA

Bella Vista, Panama City, 1944, 5 ♂, 2 juv, *Zaca*. Balboa, C.Z. 1940, 2 ♂, 1 ♀, 5 juv, *Zaca*. Balboa, C.Z., Apr. 1938, 3 ♂, 2 ♀, 8 juv Bahía Honda, 16 Mar. 1938, 3 ♂ juv, *Zaca* No. 38,701. Bahía Honda, 19 Mar. 1938, 1 ♂, *Zaca* NYZS 38,734.

ECUADOR

Puerto Bolívar, Apr. 1944, 1 ♂ juv, *Zaca*.

AMNH. 9 lots, 11 specimens.

MEXICO

Baja California: 5527, San José del Cabo, 21 Mar. 1911, 1 ♂, *Albatross*. Sinaloa: 7228, off Topolobampo, 17 Nov. 1935, 1 ♀, Templeton–Crocker Exped.

PANAMA

5405, 5408, 5419, 5434, Punta Paitilla, 26 Mar. 1926, 2 ♂, 1 ♀, 2 juv, W. G. Van Name. 5406, between Punta Paitilla and Panamá Viejo, 29 Mar. 1926, 1 ♂, W. G. Van Name. 10568, Santelmo Bay [= Ensenada Santelmo], Isla del Rey, Archipiélago de las Perlas, 15 Feb. 1941, 1 ♂, *Askoy* Exped.

PERU

Uncatalogued, Mollendo, 3 Dec. 1934, 1 ♂ juv.

BMNH. 4 lots, 8 specimens.

COSTA RICA
1892.6.7.14, Río Punta Mala, 1 ♂, H. Pittier.

PANAMA
67.77, 2 ♂, J. C. Dow.

COLOMBIA
1925.4.27.8/9, Tumaco, 1 ♂, 1 ♀ juv, R. H. Thomas.

PERU
1890.10.7.103/105, Santa Lucía, 2 ♂, 1 ♀, Stalzman collection, Warsaw Mus.

MCZ. 14 lots, 36 specimens, including the following not cited above:

MEXICO
Baja California: 5181, Cabo de San Lucas, no date, 1 ♂, J. Xantus. Guerrero: 5180, Acapulco, no date, 1 ♂, 1 ♀, *Hassler* Exped.

NICARAGUA
5178, Golfo de Fonseca, May 1869, 1 ♂, J. A. McNiel.

HONDURAS
5179, Golfo de Fonseca, recd. Nov. 1885, 5 juv, J. A. McNiel.

PANAMA
987, 15 Mar. 1869, 1 ♂, A. Agassiz. 4701, 15 Mar. 1860, 2 ♂, 1 ♀, A. Agassiz. 4702, July 1872, 1 ♂, *Hassler* Exped. 4703, recd. 13 Feb. 1861, 2 ♂, J. Rowell. 5175, Mar. 1860, 3 ♂, 2 ♀, A. Agassiz. 5176, recd. 10 June 1862, 2 ♂, 1 ♀, C. F. Davis. 5177, 4 ♂, 3 ♀, *Hassler* Exped. 8376, 12 Mar. 1891, 1 ♀ juv, *Albatross* Exped. 9669, no date, 3 ♂, Maack.

COLOMBIA
9666, Turbo?, no date, 1 ♂, Maack, Darien Exped. [Error?].

MNB. 1 lot, 4 specimens.

PANAMA
Bahía Honda, 10 Mar. 1933, 2 ♂, 2 ♀, *Velero III*, Stn. 111-33.

MNHNP. 1 lot, 6 specimens.

GUATEMALA
445a, 445d, Tanesco [= Tahuesco, 14°01′13″N, 91°07′33″W], 3 ♂, 3 ♀ (1 ov) (dry), Exp. du Mexique.

RMNH. 18 lots, 27 specimens.

MEXICO
Sonora: 7535, Guaymas, 20 May, 1945, 1 ♂, M. Cárdenas. 7529, Guaymas, 25 July 1946, 1 ♀ juv, M. Cárdenas. 7536, Yavaros, Bahía de Sta. Bárbara, 29 Nov. 1944, 1 ♂, 1 ♀ (ov), M. Cárdenas. 7532, coast of, 23 Nov. and 1 Dec. 1944, 1 ♂, 1 ♀ (ov), M. Cárdenas. Canjeme [?], 22 Nov. 1944, 1 ♀ (ov), M. Cárdenas.
Sinaloa: 7528, Ahome, 1 June 1945, 1 ♀, M. Cárdenas. 7537, Topolobampo, 21 June 1945, 1 ♀ (ov), M. Cárdenas. 7531, Macapule [Bahía de Navachiste], 22-23 Apr. 1948, 1 ♂, M. Cárdenas. 7533, Macapule, 7 May 1946, 2 ♀, M. Cárdenas.
Colima: 7534, Manzanillo, 13 Jan. 1943, 1 ♂, 1 ♀, F. Bonet.

EL SALVADOR
9839, W of Bocana Río Lempa at Isla Tasajera, San Vicente, 19 Mar. 1953, 1 ♂, 2 juv, M. Boeseman. 9840, coast at El Cuco, San Miguel, 19 Apr. 1953, 2 juv, M. Boeseman.

PANAMA
23516, Panama Canal, C.Z., 8°59.5′N, 79°30.5′W, Strand, Laagwater, 30 Apr. 1967, 1 ♂, *Pillsbury* Stn. 482. 23517, Golfo de Panamá, 8°14.3′N, 78°25.2′W-8°14.3′N, 78°25.5′W, 7 May 1967, *Pillsbury* Stn. 547.

ECUADOR
1 ♂, Frank, Cat-a.

PERU
23402, Puerto Pizarro, dept. Tumbes, Apr. 1966, 1 ♀ (ov), 1 juv, H. O. van Hagen. 23433, Paracas bight S of Pisco, 13 Apr. 1966, 2 ♂, H. O. van Hagen. 2699, 1 ♂ from Museo de Hist. Nat., Lima.

Supplementary literature records.—Bahía de Santa Elena, Ecuador (Nobili, 1901); a resume of records in Peru (Solar, Blancas, and Mayta, 1970); along Pacific coast of Colombia (Estévez, 1972).

CALLINECTES EXASPERATUS (GERSTAECKER)

Figures 9, 18g, 20i, 22g, 26

Lupea exasperata Gerstaecker, 1856, p. 129 (type: ♂, Berlin Mus. 2104 [dry], Puerto Cabello, Venezuela, Appun).

Callinectes tumidus Ordway, 1863, p. 574 [9] (syntypes: 2 ♂, MCZ 5159, Key West, Fla., J. E. Mills; 1 mature ♀, MCZ 5162, Haiti, A. Hilchenbach).- A. Milne Edwards, 1879, p. 226 (var. of *C. diacanthus*).- Rathbun, 1896, p. 359, pl. 18; pl. 24, fig. 6; pl. 25, fig. 5; pl. 26, fig. 5; pl. 27, fig. 6.- Rankin, 1898, p. 232.- Young, 1900, p. 189 (var. of *C. diacanthus*).

?*Lupa (Neptunus) diacantha*.- von Martens, 1872, p. 92 (part, the Puerto Cabello, Venezuela, specimens).

Neptunus (Callinectes) diacanthus.- Ortmann, 1894, p. 77 (part, specimen n, Haiti).

Callinectes exasperatus.- Rathbun, 1897, p. 150.- 1901, p. 49.- 1930, p. 130, text-figs. 15f, 16f, 17e, 18e, pl. 56.- 1933, p. 49.- Contreras, 1930, p. 236, fig. 7.- Chace, 1940, p. 33.- 1956, p. 154, unnumbered fig.- Chace and Hobbs, 1969, p. 131, fig. 37c.- Taissoun, 1969, p. 81, fig. 31A-D, photo 11.- 1973, p. 37, figs. 4C, 5C, photo 6.

Callinectes diacanthus.- Young, 1900, p. 186 (part).

Description.—Carapace (Figure 9) bearing four well developed frontal teeth, submesial pair narrower and slightly shorter than lateral pair. Metagastric area with posterior width 1.2-1.3 times length, anterior width 2.3-2.5 times length. Anterolateral margins strongly arched with anterolateral teeth exclusive of outer orbital and lateral spine usually but not always curved forward; teeth progressively broader laterally with fifth tooth often largest. Lateral spine stout, usually less than twice length of preceding tooth. Surface of carapace conspicuously granulate with densest concentrations on central eminences, coarsest and most widely spaced granules in front of epibranchial line separated by smooth surfaces. Central sulci on carapace definite but not deep; epibranchial line rather flatly arched, slightly sinuous.

Chelipeds robust, ridges and crests of all articles coarsely granulate; fingers of major chela strong but not markedly gaping.

Male abdomen and telson reaching along posterior quarter of thoracic sternite IV; telson lanceolate with sinuous inflated sides, length 1.5 times basal width; basal portion of fused segments 3-4-5 truncate laterally. Mature female abdomen and telson reaching about same level as in male; telson triangular with inflated sides, length 1.2 times basal width; fifth segment longer than sixth. First gonopods of male (Figures 18g, 20i) reaching slightly beyond suture between thoracic sternites VI and VII, sinuously curved, overlapping in proximal half along midline then diverging distally, twisting on axis near tip and bending abruptly mesad; armed distally with scattered minute spinules, tip slightly broadened and opening posteromesially. Gonopores of female (Figure 22g) broadly and somewhat asymmetrically ovate in outline with orientation of long axis mainly in frontal plane but with apex directed anteromesad; aperture of each laterally elongate and sinuous, sloping from broadest area at surface on mesial side to narrower and deeper portion under rounded overhanging anterior border with prominent central projection and posterior border with elongate posterolateral eminence.

Size of carapace in mm.—Largest male: length 67, width at base of lateral spines 114, including lateral spines 129. Largest female: length 59, width at base of lateral spines 101, including lateral spines 124. Summary of selected measurements is given in Tables 1 and 2.

Color.—Carapace of adult male purplish red, more accented on proto-, meso-, and metagastric areas and at base of lateral spines and anterolateral teeth; branchial region and anterolateral teeth obscure maroon. Dorsal surface of all legs purplish red with intense orange red on articulations; inferior portion of merus, carpus, and fingers of chelipeds intense violet; internal and external portion of chelae as well as entire ventral portion of animal white with tints of soft purple (Taissoun, 1969).

Variation.—There is notable variation in anterolateral tooth pattern; the fifth, sometimes described as largest (Rathbun, 1930) may be exceeded by the fourth, sixth, or a combination of both, or there may be asymmetrical size and tooth number differences.

Distribution.—Bermuda; Veracruz, Mexico; southern Florida to Estado de Santa Catarina, Brazil (Figure 26). Reason for lack of collections from the Guianas and northern Brazil is unknown.

Habitat.—This species lives primarily in shoal marine, estuarine, and perhaps fresh water, espe-

cially in association with mangroves and around river mouths from water's edge to recorded depths of about 7.5 m (Rankin, 1900; Coêlho, 1967b, 1970; Chace and Hobbs, 1969; Taissoun, 1969).

Spawning.—Few dated collections contain ovigerous females: March, Puerto Rico and Guadeloupe; April, Barbuda and Panama; May, Jamaica; June, West Indies; August, Estado de Santa Catarina, Brazil. Other undated collections in museums are from Bermuda, southern Florida, Estados de Pernambuco and São Paulo, Brazil.

Remarks.—*Callinectes exasperatus* has a number of distinctive features. It has the roughest appearing carapace and chelipeds of any species in the genus because the granulations are coarser and sharper than in others. The median epistomial tooth is more widely separated from the front than among the congeners, perhaps a function of the vaulted carapace which contributes to deep-bodied form. Similar to *C. bocourti* in structure of frontal teeth, *C. exasperatus* has less prominent cardiac lobes and sulci bounding the metagastric area. The lateral spines are relatively shorter than among other species of the genus. A blunt anteromesial eminence on the carpus is pronounced. Narrowest width of the male abdomen is in the distal third of the sixth segment, the narrowed portion becoming increasingly distal with age together with progressive crossing of the pleopods.

Dahl (1954) worked at Cañango Beach, Venezuela, at or near the type-locality for *C. exasperatus* and published a photograph of the beach at Puerto Caballo together with a short description of the area, saying that the tidal difference is small and wave exposure very great on the rather steeply sloping beach.

Locality data for specimen 303-7 in MNHNP (M. Fontaines) from "Chili" identified as *Neptunus diacanthus* Latr. (= *C. exasperatus*) is an error.

Material.—Total: 97 lots, 372 specimens.

Specimens listed in Rathbun (1930) from USNM (24463, 24464, 18631 not found) and MCZ.

USNM. 38 lots, 282 specimens, including the following not cited above:

UNITED STATES

Florida: 77125, E of Bush Key, Tortugas, 29 July 1931, 1 ♂, Pearse. 80665, Key West, no date, 1 ♂, U.S. Bur. Fish.

CUBA

77127, Bahía Honda [Pinar del Río, WSW Habana], 1 June 1893, Univ. Iowa.

JAMAICA

123077, Kingston Harbor, 17 May 1965, 1 ♀ (ov), B. B. Collette.

HAITI

71232, Muertos I., Seven Brothers group, Feb. 1929, 1 ♂, Poole and Perrygo.

PUERTO RICO

61563, Cataño [San Juan Harbor], 4 Jan. 1899, 1 ♂, *Fish Hawk*. 73281, Bahía de San Juan, 29 Mar. 1937, 1 ♂, W. L. Schmitt. 123084, Boca de Cangrejos, 7 mi E San Juan, 31 Mar. 1937, 1 ♂, 2 ♀ (1 ov), W. L. Schmitt.

VIRGIN ISLANDS

71639, St. Croix, no date, 1 ♂, H. A. Beatty. 72353, St. Croix, 1935-36, 2 ♂, H. A. Beatty. 76466, St. Croix, no date, 1 ♀, H. A. Beatty.

BARBUDA

123079, west shore of lagoon near Oyster Pond Landing, 6 Apr. 1956, 1 ♀ (ov), Schmitt, Chace, Nicholson, and Jackson, Stn. 85-56, *Freelance*.

GUADELOUPE

123080, between Monroux and Rat Is., Pointe a Pitre, 30-31 Mar. 1956, 3 ♂, 2 ♀ (1 ov), Chace and Nicholson, Stn. 68-56, *Freelance*.

GRENADINES

123078, Tyrrell Bay, Carriacou I., 16 Mar. 1956, 2 ♂, D. V. Nicholson, Stn. 17-56, *Freelance*.

MEXICO

Quintana Roo: 78391, Bahía de la Ascensión, 28 Mar. 1939, 1 ♂, Ralph Elliott. 123082, N end Bahía de la Ascensión, 15 Apr. 1960, 3 ♂, 1 ♀, Daiber and Schmitt. 123083, Bahía de la Ascensión behind Pta. Allen, 16 Apr. 1960, 1 ♂, Daiber and Haynes. 123081, Bahía del Espíritu Santo, near Pta. Lawrence, 6 Apr. 1960, 1 ♀, Rehder, Daiber and Haynes.

VENEZUELA

95713, Gran Roque, Los Roques Is., 7 Sept. 1950, 1 ♂, F. H. Weibezahn.

AHF. 3 lots, 4 specimens.

UNITED STATES
Florida: Key Largo, North Hawk Channel, 29-31 May 1949, 2 ♂, Stn. LM 25, 27. Hawk Channel, Plantation Key, 3 mi S Tavernier Bridge, 25 May 1949, 1 ♂, Stn. LM20-49.

TRINIDAD
Purchased from fisherman near Port of Spain, 17 Apr. 1939, 1 ♀.

AMNH. 4 lots, 4 specimens.

BERMUDA
11223, 1939, 1 ♀ (ov), W. Beebe, Bermuda Exped.

BAHAMAS
2286, Andros, 1908, 1 ♀, B. E. Dahlgren and H. Mueller.

PUERTO RICO
2673, San Juan, entrance of Bahía de Condado, 14 July 1914, 1 ♀, R. W. Miner. 2661, July-Aug. 1914, 1 ♂ (dry), R. W. Miner.

ANSP. 1 lot, 1 specimen.

BRAZIL
3514, no date, 1 ♀ (dry), T. B. Wilson.

BMNH. 7 lots, 12 specimens.

UNITED STATES
Florida: 1938.3.19.22, Dry Tortugas, 1 ♂, Colman and Tandy.

BRITISH HONDURAS
1967.7.1.49/50, Long Cay Island, 23/10/1941, 1 ♂, 1 ♀, I. Sanderson.

CAYMAN ISLANDS
1955.10.6.59, Stn. 33, 1 ♂, Oxford Univ. Exped.

JAMAICA
vi/8, no date, 2 ♂, 2 ♀ (dry), Banks.

BRAZIL
80.37, Pernambuco, no date, 2 ♂, W. Forbes. 61-44, vi/7, Rio de Janeiro, no date, 1 ♂ (dry), U.S. Explor. Exped. 919/C, vi/7, no date, 1 ♂ (dry), C. Stewart Banks.

MCZ. 14 lots, 26 specimens.

UNITED STATES
Florida: 5160, Key West, no date, 1 ♂ (juv), 1 ♀ (ov), J. E. Mills.

BAHAMAS
Bimini: 11671, Alicetown, May 1941, 1 ♂, R. W. Foster and J. Huntington. 11692, Nixons Harbour, May 1941, 1 ♂, R. W. Foster and J. Huntington. 10360, Great Inagua I., Salt pond canal 1½ mi SE Matthew Town, 24 June 1938, 1 ♂, 1 ♀, R. H. McLean and B. Shreve.

CUBA
10889, Bahía de Siguanea, Isla de Pinos, 14 Feb. 1938, 1 ♂, 1 juv, Harvard-Havana Exped.

BRAZIL
5167, Santos, Estado de São Paulo, no date, 1 ♀ (ov), Coutinho, Thayer Exped.

MNB. 6 lots, 9 specimens.

BRAZIL
56, Pernambuco, no date, 1 ♂, 2 ♀ (ov). 58, Rio Guanabara, no date, 1 ♂. 52, Rio Guanabara, no date, 2 ♂. 1380, Baía de Guanabara, 1948, 1 ♂, P. Drach. Estado de Santa Catarina: 59, São Francisco do Sul, 1901 (?), 1 ♀, L. Gralberto. 499, no data, 2 ♀.

MNHNP. 2 lots, 2 specimens.

QUESTIONABLE LOCALITIES
Suitrée(?), 1922, 1 ♂, from Museo de Historia Natural, Buenos Aires. Chili(?), 303-7, no date, 1 ♀ (dry), M. Fontaines.

RMNH. 17 lots, 26 specimens.

UNITED STATES
Florida: 15631, Key Biscayne, Miami, 14 Sept. 1960, 1 ♂, R. B. Manning and L. B. Holthuis.

WEST INDIES
2326, June 1920, 1 ♀ (ov), J. Boeke.

ST. MARTIN
11879, Baie Orient, 23 Feb. 1957, 1 ♂, L. B. Holthuis.

ARUBA
15044, 1882-1883, 2 ♂ (juv), A. J. van Koolwijk.

CURAÇAO

St. Kruis Baai, 7 Oct. 1948, 1 carapace (dry), P. W. Hummelinck. 15056, shore of Piscadera Baai near Raphaël, 13 Nov. 1956, 1 (juv), L. B. Holthuis. 11877, Piscadera Baai, 27-28 Dec. 1956, 1 ♂, 2 ♀, 3 juv, L. B. Holthuis. Schottegat at Pasanggrahan, 22 Aug. 1948, 1 ♀ (dry), P. W. Hummelinck. South shore St. Joris Baai near Choloma, 3 Jan. 1957, 1 ♀ (dry), L. B. Holthuis. 11878, South shore St. Joris Baai near Choloma, 3 Jan. 1957, 1 ♂, 1 ♀, L. B. Holthuis.

BONAIRE

11880, lake on E coast, 10 Mar. 1957, 1 ♂, 1 ♀, L. B. Holthuis. 11876, lake on E coast, 6 Mar. 1957, 1 ♂, L. B. Holthuis. Paloe Lechi, 6 Apr. 1955, 1 carapace (dry), Zaneveld.

TRINIDAD

23413, Cocorite, 25 Aug. 1965, 1 ♂, 1 ♀, H. O. von Hagen.

VENEZUELA

10719, Isla de Margarita, Feb. 1955, 1 ♂, J. S. Zaneveld. 23396, Punta Mangle, Isla de Margarita, 11 Jan. 1964, 1 ♂, P. W. Hummelinck.

BRAZIL

4873, Bahia, 1909, 1 ♂, J. A. Bierens de Haan, Zool. Lab. Utrecht.

SADZ-B. 5 lots, 6 specimens.

BRAZIL

Bahia: 3223, Ilhéus, 1919, 1 ♂, 1 ♀, E. Garbe. 3214, Ilha Madre de Deus, Jan. 1933, 1 ♂. Rio de Janeiro: 3242, Atafona, 12 July 1963, 2 juv, N. Meneses. 3246, Atafona, no date, 1 ♂, N. Meneses. Santa Catarina: 3245, 27°15'S, 48°47'W, near Florianópolis, 21 Aug. 1966, 1 ♀ (ov), M. Iwai.

UNC-IMS. 1 lot, 3 specimens.

PUERTO RICO

2137, Mangrove channels behind Bahía Fosforescente, 2 May 1967, 2 ♂, 1 ♀, D. R. Torres and P. R. Ramos.

Supplementary literature records.—Southern Florida, Futch (1965); Biscayne Bay, Fla. (Park, 1969); Veracruz, Ver., Mexico (Contreras, 1930); Jamaica (White, 1847); Golfo de Venezuela (Taissoun, 1969); Gran Roque, Venezuela (Chace, 1956); Jangadas, south of Recife, and other localities in Pernambuco, Brazil (Coêlho, 1966, 1967b); Texas ? (tentatively identified specimen not available for confirmation, Pounds, 1961).

CALLINECTES BELLICOSUS (STIMPSON)

Figures 10, 18h, 20j-k, 22h, 27

Lupa bellicosa (Sloat, MS) Stimpson, 1859, p. 57 [11] (type locality: Guaymas, Gulf of California, C. P. Stone, types not extant).- ? Lockington, 1876, p. 105 [11].

Callinectes bellicosus Ordway, 1863, p. 577 [12].- Streets and Kingsley, 1878, p. 107.- A. Milne Edwards, 1879, p. 227 (var. of *C. diacanthus*).- Rathbun, 1896, p. 365, pl. 22; pl. 24, fig. 10; pl. 25, fig. 8; pl. 26, fig. 8.- 1898, p. 596.- 1926, p. 75 [Signal Hill Pleistocene].- 1930, p. 112, text-figs. 15k, 16i, 17g, 20, pl. 49.- Holmes, 1900, p. 73.- Young, 1900, p. 190 (var. of *C. diacanthus*).- Schmitt, 1921, p. 236, text-fig. 140.- Meredith, 1939, p. 108 [figure].- Steinbeck and Ricketts, 1941, p. 468, pl. 14, fig. 2.- Buitendijk, 1950, p. 275.- Garth and Stephenson, 1966, p. 47, pl. 5, fig. B; pl. 8, fig. B; pl. 10, fig. B; pl. 12, fig. B.- ? Contreras, 1930, p. 240, text-fig. 11.

Callinectes diacanthus.- Young, 1900, p. 186 (part).

Callinectes ochoterenai Contreras, 1930, p. 229, text-figs. 2, 3A-C (type localities: LaPaz, Baja California, and Punta Arena, Guaymas, Sonora [Mexico]).

Description.—Carapace (Figure 10) with two slender frontal teeth separated by a space often bearing a rudimentary submesial pair of teeth; median epistomial spine below front prominent and slightly exceeding frontal teeth. Metagastric area with lateral sulci fairly deep but anterior and posterior margins obsolescent, posterior width greater than length. Inner orbital fissure usually open. Anterolateral margins broadly arched, teeth exclusive of outer orbital and lateral spine relatively short and concave sided with acuminate tips directed outward more than forward; lateral spines short, about twice length of preceding tooth, longer in juveniles. Surface finely granulate and remarkably smooth except on anterolateral

region where granules are more widely spaced; sulci and lines of granules more prominent on young than on adults.

Chelipeds with prominent and sharply tuberculate or spiniform ridge on outer surface of propodus, other ridges lower and nearly smooth.

Male abdomen and telson reaching a bit beyond suture between thoracic sternites IV and V; telson triangular, longer than broad, sixth segment slightly constricted in proximal half. Mature female abdomen and telson reaching about same level as male, telson with inflated sides longer than wide, segments 5 and 6 almost equal in length. First gonopods of male (Figures 18h, 20j, k) reaching to midlength of thoracic sternite VI with tips slightly inclined mesad toward each other, not overlapping but thrown into sinuous curves, twisting on axis at level of suture between thoracic sternites VI and VII and armed at this level with a crowded lateral band of assorted short, rather blunt, retrogressive spinules becoming less numerous and more slender proximal and distal to this level, longer distally and shorter proximally; a subterminal row of rather prominent well separated exceedingly slender setae on sternomesial aspect. Gonopores of female (Figure 22h) asymmetrically ovate in outline with orientation of long axis mainly in frontal plane but with apex directed anteromesad; aperture of each laterally elongate and sloping from broadest area at surface on mesial side to narrower deeper portion under uniformly rounded borders on remaining sides.

Size of carapace in mm.—Largest male: length 76, width at base of lateral spines 135, including lateral spines 154 (from crab purchased in Mexico City fish market by Edgard Taissoun and Alfredo Vidal after statistical analysis was completed). Largest female: length 89, width at base of lateral spines 160, including lateral spines 178. Summary of selected measurements is given in Tables 1 and 2.

Color.—The only good published color description is that of Garth and Stephenson (1966), "Carapace mottled greenish yellow to brownish green, sometimes with dark spot on center of orbit and dark green areas roughly outlining epibranchial ridge. Arms generally greenish yellow to greenish brown, wrist articulations purple red. Hand with blotch at level of finger articulation, this blue-green in smaller and purple in larger specimens. Similar internal blotch purple throughout. Inner surface hand and fingers centrally white to pale blue, dorsally purple to red-purple, and ventrally blue to purple-blue. Cheliped colors most vivid in largest male." Almost brown above, cream colored below, tubercles and ridges of hand tinged with red (Lockington, 1876).

Specimens purchased at a fish market in Mexico City and preserved in Formalin[2] about 21 June 1972, by Edgard Taissoun and Alfredo Vidal were seen by me on June 23. Colors were: male tannish purple overall; ridges of chelipeds, carpi, and front edge of meri having deepest purplish cast. Posterior areas of carapace grading through brownish cast to areas of beige on posterolateral slopes and swimming paddles. A round beige spot on posterolateral border just anterior to insertion of swimming legs. Upper surfaces of palms with a reticulate pattern of purple lines on beige to off-white background. Inner and outer surfaces of chelipeds and ventral aspect off-white with suggestion of yellow. Superior and inferior edges of fingers purple grading to blue on inner face of fingers, and a reticulate blue stripe along lower inner border of palm. Teeth of chelipeds oyster white at their crowns, but their bases light purple giving impression of a purple "gum" line.

Female similar to male but with a more tan to beige hue on carapace and upper surface of palms. Blue color confined to inner surface of propodal finger only.

Prominent tubercles and tips of spines oyster white in both sexes.

Variation.—Variation in *C. bellicosus,* as in other members of the genus, seems largely a matter of differential growth changes. Openness of the inner orbital fissures has been used as a key character for this species, but large series show the character to vary individually; though usually open, the fissure is often closed. The edge of the frontal area slopes upward from contact with the exposed median epigastric spine to a row or cluster of obsolescent granules which mark the site of obsolescent submesial frontal teeth. In all other species the front overhangs this spine to at least some extent. The species is notable for sharpness of teeth and spines. Anterolaterals pointing forward in the young are directed more outward in mature specimens. These teeth are often almost

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

rectilinear but still sharp tipped. Sub- and outer orbital spines become increasingly acuminate with age. The mesogastric area changes shape with age, the anterior border becoming increasingly sinuous and indistinct. Adjacent portions of the mesobranchial regions remain sharply outlined in old individuals. Some older specimens show "expansion scars" on the carapace as if stresses incurred while molting had stretched the carapace during the hardening process. Such "scars" seem to radiate from centers in the cardiac region.

The chelae sometimes have lower propodal margins slightly decurved in conjunction with development of a strong basal tooth on the opposing dactyl. Except for the sharply granulate outer propodal ridge, usually smooth remaining ridges on the chelipeds are occasionally as roughly granulate as in *C. exasperatus*.

In sternal view, males have a great resemblance to *C. similis* in that the abdomen and sternum are nearly plane and that the anterior curvature of fused segments 3-5 is shallow. Males may show a central proximal column of indurated exoskeleton in the 6th abdominal segment. The first gonopods of mature males may reach beyond the middle of sternite VI to the suture between V and VI.

Distribution.—San Diego, Calif., to Bahía Almejas (southeastern extension of Bahía Magdalena) Baja California; La Paz Harbor around Golfo de California to Topolabampo, Sinaloa, Mexico (Figure 27). The species is apparently absent from the extreme southern tip of Baja California, but was listed as the commonest large crab in the Golfo de California by Steinbeck and Ricketts (1941).

Habitat.—Garth and Stephenson (1966) summarized the little available ecological data noting that the known depth range is 0 to 18 m, usually over sand bottom, and that many crabs had been captured swimming under lights at night. From museum records it is clear that the species frequents estuarine areas. A few specimens from Espíritu Santo, Golfo de California (AHF) are covered with a red clay deposit.

Spawning.—Only one lot taken in September from Scammon Lagoon, Baja Calif., in water 0.6 m deep contained ovigerous females. This is curious in light of the fact that more mature females have been collected than males (Tables 1 and 2), but the record is probably biased by times of collection. Of 94 lots for which collection date is recorded, the monthly frequency is: January 5, February 11, March 43, April 17, May 3, June 2, August 3, September 2, October 1, November 5, and December 2. Either spawners were beyond depths sampled (unlikely) or early spring is not the main spawning period for this species.

Economic importance.—No data are available on uses of this crab other than notes above on its availability in fish markets of Mexico City. Thirteen lots of fragments, mostly parts of fingers, from archeological sites near Municipio Caborca, La Cholla Bay, Sonora, Mexico, are recorded in the USNM as *Callinectes* (probably *C. bellicosus*) indicating pre-Columbian use of the large crabs by peoples of the area.

Remarks.—*Callinectes bellicosus* resembles *C. similis* of the Carolinian province of the Atlantic in that both are restricted in distribution at the northern fringes of the tropical homeland of the genus, but the analogy is a loose one for *C. bellicosus* is the more restricted, essentially endemic to the Golfo de California which is a transitional body of water with Panamanian relationships grading from tropical in the south to temperate (but warm in summer) in the north, and the Pacific coast of the Baja California peninsula whose marine climate is transitional between tropical and dominant temperate from Punta Entrada (Bahía Magdalena) to Point Conception north of Santa Barbara Channel (Garth, 1961a). Temperate and tropical faunas meet and mingle along this outer coast, but tropical forms thin out northward surviving only in protected shallows. Records of *C. bellicosus* are few north of Scammon Lagoon, northern extensions of range being favored by warm periods (Garth, 1961a). The southern tip of the peninsula, from which *C. bellicosus* is absent, is essentially an insular oceanic region distinct from adjacent coastlines and dependent on accidental transport for its marine fauna (Garth, 1961a).

Belonging to the group of species with moderately long first gonopods, *C. bellicosus* has diverged from the remainder of the group in having gonopods with rather straightened sinuosity and possession of prominent sternomesial setae. The form of the body bears some resemblance to *C. similis*, the distributional western Atlantic

analog, in having a smooth and finely granulate carapace, reduced submesial frontal teeth, shallow anterolateral teeth, nearly plane sternum and abdomen in males, and similar length-width proportions in mature males.

A Pleistocene record for *C. bellicosus* (USNM 372804) is represented by the distal two-thirds of a propodal finger from a minor left chela of a large crab from the upper San Pedro formation, Signal Hill, northeast of Long Beach, Calif. (Rathbun, 1926). Size and tooth pattern of this specimen are indistinguishable from the modern form.

Material.—Total: 87 lots, 322 specimens.

Specimens listed in Rathbun (1930) from USNM (4630 not found) and AMNH; Garth and Stephenson (1966) from AHF and USNM.

USNM. 32 lots, 137 specimens, including the following not cited above:

MEXICO

Baja California: 12464, [?] 3 ♂, col. unknown. 63280, S end Bahía Magdalena, 20 Mar. 1911, 4 ♂, *Albatross*. Uncatalogued, Ricason I., Bahía Concepción, 7 Apr. 1911, 3 ♂, *Albatross*. 60006, Bahía Concepción, mouth of Rio Mulegé, 4 Apr. 1911, 1 ♂, *Albatross*. 57909, Bahía de los Angeles, 1921, 1 ♂, Calif. Acad. Sci. Sonora: 80666, Bay at Guaymas, 31 Jan. 1923, 1 ♂, 2 juv, B. F. Yost. 97611, Estero de Agiabampo, no date, 1 ♂ (dry), E. F. Ricketts. 81926, 1 ♂, 2 ♀, 7 juv. 122921, Agiabampo, May 1939, 1 ♀, R. Hermosillo.

AHF. 44 lots, 158 specimens.

AMNH. 4 lots, 18 specimens, including the following not cited above:

MEXICO

Baja California: 5498, Bahía Tórtolo, Punta San Bartolomé, 14 Mar. 1911, 1 ♂, *Albatross*. 5508, Bahía Ballenas, 16 Mar. 1911, 2 ♂, 1 ♀, *Albatross*. 5524, Bahía Magdalena, 20 Mar. 1911, 6 ♂, 2 ♀, *Albatross*. 5504, Bahía Pichilinque, 27 Mar. 1911, 3 ♂, 3 ♀, *Albatross*.

BMNH. 1 lot, 1 specimen.

79.1, off San Francisco, 1 ♂, E. Gerrard, Jr. [Error, or San Francisco I., 24°50′N, 110°35′W, G. de Calif.?].

MCZ. 1 lot, 3 specimens.

MEXICO

Baja California: 4253, Shoal Point, Colorado River, 29 Mar. 1889, 2 ♂, 1 ♀, *Albatross*.

RMNH. 4 lots, 4 specimens.

MEXICO

Baja California: La Paz, 15 Oct. 1945, 1 ♀, M. Cárdenas. Sonora: 7540, Guaymas, 25 Sept. 1945, 1 ♀, M. Cárdenas. Sinaloa: 7538, Ahome, 1 June 1945, 1 ♀, M. Cárdenas. 7539, Topolobampo, 21 Apr. 1945, 1 ♂, M. Cárdenas.

Los Angeles County Museum. 1 lot, 1 specimen.

MEXICO

Baja California: Bahía Santa María, Mar. 28, year unknown, 1 ♀, A. E. Colburn, A748.

Supplementary literature record.—Punta Santa Inés [Baja Calif.] (Crane, 1937).

CALLINECTES TOXOTES ORDWAY

Figures 11, 18i, 20l, 22i, 27

?*Callinectes diacanthus* Stimpson, 1860, p. 220.

Callinectes toxotes Ordway, 1863, p. 576 [11] (syntypes: ♂, USNM 2413: 2 ♂, MCZ 5182; ♂ [dry], MCZ 5183; Cape San Lucas [Baja California], John Xántus, col.).- A. Milne Edwards, 1879, p. 227 (var. of *C. diacanthus*).- Rathbun, 1896, p. 363, pl. 21; pl. 24, fig. 9; pl. 25, fig. 9; pl. 26, fig. 9; pl. 27, fig. 8.- 1910, p. 536, pl. 55.- 1930, p. 127, figs. 15i, 16g, 17i, 18h, pl. 54.- Young, 1900, p. 189 (var. of *C. diacanthus*).- Contreras, 1930, p. 237, fig. 8.- Garth, 1948, p. 35.- 1957, p. 37.- 1961b, p. 142.- Garth and Stephenson, 1966, p. 50, pl. 5, fig. C; pl. 8, fig. C; pl. 10, fig. C; pl. 12, fig. F.- Bott, 1955, p. 56.

Callinectes robustus A. Milne Edwards, 1879, p. 227 (var. of *C. diacanthus*) (type locality: Colombia; type listed by Rathbun, 1930, in MNHNP, not found in 1968, considered lost, 1973, fide J. Forest).- Young, 1900, p. 189 (var. of *C. diacanthus*).

Callinectes diacanthus.- Young, 1900, p. 186 (part).

Description.—Carapace (Figure 11) bearing four large, rounded frontal teeth; submesial pair narrower than, partially coalesced with, and reaching half the length or more of lateral pair.

Metagastric area with length approximately equal to posterior width, anterior width about 2 times length. Anterolateral margins moderately arched, teeth exclusive of outer orbital and lateral spine varying from triangular or inflated triangular at inner end of row through acuminate forward trending intermediate teeth to forward curving spiniform tooth at outer end of row, base of first and last tooth narrowest. Surface of carapace coarsely granulate and uneven, nearly smooth around margins and along regional sulci, more granulate over branchial and gastric areas, most closely crowded granules on cardiac, mesobranchial, and anterior half of mesogastric regions. Epibranchial line prominent and nearly uninterrupted.

Propodus and carpus of chelipeds with sharply and rather coarsely granulated ridges, especially on propodus, rarely worn smooth; dactyl of major chela with basal teeth (often a single strong tooth) closing against cuspate molariform complex on propodus, both chelae with sectorial teeth.

Male abdomen and telson reaching beyond midlength of thoracic sternite IV; telson much longer than broad, triangular with inflated sides; sixth segment of abdomen narrowest in proximal third. Mature female abdomen and telson reaching no more than midlength of thoracic sternite IV; telson elongate triangular with inflated sides, sixth segment longer than fifth. First gonopods of male (Figures 18i, 20l) very long, reaching to or beyond suture between thoracic sternites IV and V; sinuously curved, overlapping proximally, diverging distally, twisting mesioventrally on axis at midlength of thoracic sternite V and recurving to termination near midline; armed distally with lateral band of retrogressive spinules thinning to absence near tip. Gonopores of female (Figure 22i) asymmetrically and narrowly ovate in outline with apex on long axis directed anteromesad; rounded borders with series of wrinkles conforming to contours; aperture of each sloping from surface on mesial side under anterolateral border superior to a rounded eminence on posterior border.

Size of carapace in mm.—Largest male: length 88, width at base of lateral spines 156, including lateral spines 193. Largest female: length 74, width at base of lateral spines 133, including lateral spines 174. Estévez (1972) reported a female with carapace 75 mm long estimated to have a width including lateral spines of 182 mm, and estimated general growth rate per molt to be 15% in length, 24% in width. Summary of selected measurements is given in Tables 1 and 2.

Variation.—This species attains the largest size in the genus, but old individuals apparently do not show teeth or spines worn to an extent comparable with other species. Anterolateral teeth vary individually in degree of laterally progressive upturning in the row. Submesial frontal teeth vary considerably in length as well as acuity, but none are really sharp pointed. Chelae in seemingly old individuals retain basal teeth with well defined molariform structure on the major hand; sectorial tooth development seems more prominent on both right and left chelae than in other species. Females have granules more prominent and closely crowded on the carapace than males. Male first gonopods cross over each other at the tips in some individuals.

Distribution.—Cabo de San Lucas, Baja California, to extreme northern Peru; extraterritorial, Juan Fernández (Figure 27).

Habitat.—Ranging from shore to 27-m depths, *C. toxotes* has been characterized as a mangrove swamp crab (Estévez, 1972). It occurs from freshwater streams to open bays, and a number of collections come from lagoons or river mouths.

Stomachs of 521 specimens contained bivalves, gastropods, inorganic debris, crustaceans, fishes, and polychaetes in order of precedence (Estévez, 1972).

Spawning.—Material available for study includes only three ovigerous females: January, Panama; August, Acapulco, Mexico; a third undated specimen from Cabo San Lucas, Baja California, in MCZ was collected by John Xántus, perhaps with the type material.

Only one–third of the specimens of *C. toxotes* in museum collections are sexually mature, and among these males outnumber females 2:1. The small number of ovigerous females should therefore not cause surprise.

Economic importance.—The species is used as food and sold at the market of Buenaventura, Colombia. Crabs there are brought from Málaga Bay and others, many (mostly immature) being caught by shrimpers along the coast (Mario Estévez, pers. commun.). Collections from Estados de Sinaloa and Nayarit, Mexico; Tumaco, Colombia;

and Guayaquil, Ecuador; are from places where fishing is active or from fish markets.

Remarks.—The type locality lies at the extreme northern end of the distributional range, seemingly so far removed from the remainder of the range that one might question origin of the syntypes. Xántus (Madden, 1949) was an excellent and energetic collector for the Smithsonian Institution who lived and worked at Cabo de San Lucas from 4 Apr. 1859 to 7 Aug. 1861. Collectors then were not so precise about recording locality data as today, and Xántus was no exception. It is known that collections were brought to Xántus from Bahía Magdalena to the north and Revillagigedo Island to the south, etc., and that he visited Mazatlán on the mainland in summer, 1861, returning to Cape San Lucas on 1 Aug. Though no collection date is recorded with the types, MCZ received its specimens from the Smithsonian Institution on 13 Feb. 1861, which would seem to limit origin of the specimens to the tip of Baja California or at least rule out collection on the mainland closer to the rest of the range for the species. Moreover, an ovigerous female bearing a Cabo de San Lucas label (MCZ 5184), received with the mature types, suggests a breeding population and not an accidental occurrence.

Usual habitat of the species suggests that the Juan Fernández collection is extraterritorial. Set of currents between this isolate and the nearest known population in Peru suggest that if a breeding population does exist there, it is introduced. Further collecting both here and in the Cabo de San Lucas area would be useful.

Material.—Total: 30 lots, 120 specimens.

Specimens listed in Rathbun (1930) from USNM and MCZ; Garth and Stephenson (1966) from AHF and USNM.

USNM. 19 lots, 44 specimens, including the following not cited above:

MEXICO

Sinaloa and Nayarit: 61023, 1926, 1 ♂ (dry), C. Stansch, No. 33.

COSTA RICA

112356, Golfo de Nicoya, Jan. 1952, 2 carapaces (dry), S. E. Erdman.

PANAMA

73283, Bahía Honda, 9 Mar. 1933, 1 juv, W. L. Schmitt. 122920, no date, 1 ♂.

COLOMBIA

77045, Buenaventura, 18 Nov. 1934, 1 ♀ juv, R. Mensing.

AHF. 8 lots, 44 specimens, including the following not cited above:

[Nicaragua material Stn. 962-39 = a *Portunus* species].

COSTA RICA

Bahía Carrillo, 6 Feb. 1938, 1 ♂, *Zaca* Stn. 208, NYZS 38,194. Golfito, Golfo Dulce, 6 Mar. 1938, 1 ♂, *Zaca*, NYZS 38,525.

MCZ. 5 lots, 28 specimens, including the following not cited above:

MEXICO

Baja California: 5184, Cabo de San Lucas, no date, 1 ♀ (ov), J. Xántus. (recd. from Smithsonian Inst. 13 Feb. 1861). Guerrero: 5185 and 8755, Acapulco, Aug. 1872, 9 ♂, 15 ♀ (1 ov), *Hassler* Exped.

AMNH. 1 lot, 3 specimens.

COLOMBIA

10587, Tumaco, 19 Apr. 1941, 2 ♂, 1 ♀, *Askoy* Exped.

RMNH. 1 lot, 1 specimen.

Cat. a. South America, 1 ♂ (dry), Latreille.

Supplementary literature records.—Acapulco, Guerrero, Mexico (Contreras, 1930); Acajutla, Barra Ciega, La Libertad, La Unión, El Salvador (Bott, 1955); NW Corinto, Nicaragua (Garth and Stephenson, 1966); Baudó, Juanchaco, Catripe, Togoromá, Málaga, Buenaventura, Guapi, San Juan del Sur, Cabo Manglares, Punta Coco, and Tumaco, Colombia (Estévez, 1972).

CALLINECTES BOCOURTI A. MILNE EDWARDS Siri (Brazil)

Figures 12, 18j, 20m, 22j, 27

Cancer pelagicus.- de Geer, 1778, p. 427, pl. 26, figs. 8-11.

Callinectes bocourti A. Milne Edwards, 1879, p. 226 (syntypes: 2 ♂, MNHNP, Mullins River, 20 miles south Belize, [British] Honduras, M. Bocourt).

Callinectes Cayennensis A. Milne Edwards, 1879, p. 226 (syntypes: 2 ♂, MNHNP [French] Guiana, M. Mélinon).

Lupa diacantha.- Kappler, 1881, p. 143.

?*Neptunus diacanthus*.- Thallwitz, 1892, p. 53.

Callinectes bocourti.- Rathbun, 1896, p. 369, pls. 19; 24, fig. 7; 25, fig. 6; 26, fig. 6; 27, fig. 6 [part].- 1897, p. 151 [part].- 1901, p. 49.- 1930, p. 128, text-figs. 15g, 16e, 17h, 18f, pl. 55.- 1933, p. 49.- 1936, p. 383.- Young, 1900, p. 192.- Bott, 1955, p. 56.- Holthuis, 1959, p. 201, text-fig. 47, pl. 5, fig. 2.- Chace and Hobbs, 1969, p. 127, text-figs. 35, 37a.- Taissoun, 1969, p. 57, figs. 20A-D, photo 7.- 1972, p. 31, figs. 1a-d, 2 [part], 3 [part], 9C, 10C-D; photos 4b, 5-6, (col.), 7.- 1973, p. 24, figs. 4G, 5G, photo 2.

Callinectes diacanthus.- Young, 1900, pls. 2, 3.

Callinectes cayennensis.- Young, 1900, p. 192.

Callinectes danae.- Tesch, 1914, p. 195 (fide, Holthuis, 1959, p. 205).

Description.—Carapace (Figure 12) bearing four triangular frontal teeth with tips reaching a nearly common level, lateral pair obtuse with mesial side having flatter angle than lateral side, submesial pair narrower than laterals. Metagastric area with length and posterior width about equal, anterior width 2 times length. Anterolateral margins moderately arcuate, anterolateral teeth exclusive of outer orbital and lateral spine swept forward, anterior margin of teeth shorter than posterior margin, teeth in lateral half of row always acuminate. Surface of carapace dorsally smooth and glistening around perimeter (when wet) and on epibranchial surfaces; central portion granulate, coarsest granules over mesobranchial and rear half of cardiac areas and lateral half of branchial lobes. Epibranchial line prominent and nearly continuous, sulci on central part of carapace deeply etched.

Chelipeds remarkably smooth except for usual spines and obsolescent granules on ridges; fingers of major chela heavily toothed, lower margin of propodal finger often decurved near base in adults.

Male abdomen and telson long, extending nearly to juncture between thoracic sternites III and IV; telson lanceolate, much longer than broad; sixth segment of abdomen broadened distally. Mature female abdomen and telson reaching as far forward as in male, sixth segment nearly as long as fifth, its distal edge uniformly arched, telson elongate-triangular with inflated sides. First gonopods of male (Figures 18j, 20m) very long, often exceeding telson and crossed near tips; sinuously curved and overlapping in two places proximally, diverging distally, twisting mesioventrally on axis lateral to abdominal locking tubercle and recurving gradually to termination near midline; armed distally with a dorsolateral band of large and small retrogressive spinules. Gonopores of female (Figure 22j) asymmetrically ovate in outline with apex on long axis directed anteromesad; aperture of each sloping from surface on mesial side under rounded, sinuous anterolateral border superior to a low rounded eminence on posterior border.

Size of carapace in mm.—Largest male: length 76, width at base of lateral spines 132, including lateral spines 156. Largest female: length 70, width at base of lateral spines 121, including lateral spines 146. Summary of selected measurements is given in Tables 1 and 2. The species characteristically reaches fairly large size.

Color.—Complete color descriptions (Chace and Hobbs, 1969; Taissoun, 1969, 1972) and notes (Rathbun, 1896, 1930; Holthuis, 1959) give a range of color variations. These can be broadly summarized as: Overall cast olive green with prominent reddish markings. Carapace olive, grayish green, greenish chestnut, or forest green with variable purplish to red markings, especially on branchial, hepatic, cardiac, and gastric areas, individuals of large size sometimes being dark chestnut tinted blackish brown on gastric and metagastric areas, with an oblique spot on subbranchial region; anterolateral teeth olive green with brown to red tints and yellowish white tips. Chelipeds red to dark reddish brown above and whitish below with bluish tints, main colors being sharply separated on outer surface of palm; fingers red to reddish brown, a purplish cast on internal articulation of merus with carpus and this member with chela; tubercles, tips of fingers, and spines on articles cream. Remaining legs reddish above with shades of maroon, yellow, and olive green ventrally except distal articles scarlet to red or dark red distally; hairs olive-tan. Underparts of body mainly dirty white to purplish red with suffusion of blue marginally, first abdominal seg-

ment mainly reddish tan. Males tend to be reddish, females greenish.

Variation.—This species greatly resembles both *C. rathbunae* and *C. maracaiboensis* but generally has more obtuse frontal and anterolateral teeth as well as more pronounced smoothness on chelipeds and carapace. Considerable variation attributable to growth and age is evident. The submesial pair of frontal teeth become relatively more slender with age, but seldom extremely acute. Some young have quite lobate frontals, scarcely separated; an extreme case is represented by MCZ lot 5186 from Caruca, Rio Maria [= Rio Caraçaua near Belem?] Brazil, in which an immature female has lobate frontal teeth partially coalesced while more mature males in the lot have fairly sharp submesial frontals. There is great variation in length of lateral spines, the relationship of spine length to that of the last anterolateral tooth as cited by Rathbun (1930) and Taissoun (1972) not holding up as a key character for large series of specimens. Anterolateral teeth vary from obtuse to acuminate, acuteness increasing somewhat with age, and edges of the teeth vary from smooth to granulate with greatest amount of granulation usually on the posterior margin. There is more apparent variation in chelipeds than among other species of the genus. A character accentuated with age, especially among males, is a major cheliped with gaping fingers in which the propodus is decurved along its lower margin. At one extreme is a heavy gaping hand with strong basal tooth on the dactyl, whereas at the other both chelae may be slender and almost symmetrical. Many individuals have a major chela that is halfway along this scale of development; others possess two minor chelae of nearly uniform size—evidence of regeneration.

From Rio de Janeiro south, specimens seen have stronger and more sharply granulate ridges on the chelae than those from other parts of the species' geographic range. Likewise on these southern forms, granules are bold on the posterior slope of the cardiac area and sometimes crowded into suggestion of a transverse ridge at summits of the cardiac and mesobranchial areas. Both developments are reminiscent of similar patterns found in the acutidens form of *C. sapidus*. Frontal teeth, mesogastric area, and first pleopods of these forms seem typical of *C. bocourti*.

More obscure are other variations which have bearing on the separation of *C. bocourti* from *maracaiboensis*. A series of variant specimens from over the geographic range of *C. bocourti* demonstrate these.

Brazil: An ovigerous female from Praia Inglese, São Francisco (USNM 60978) has its sixth abdominal segment relatively narrow for its length with the distolateral edge angular (typical), not rounded as in *C. maracaiboensis*, the anterolateral teeth sharp and not curved forward, and the frontal teeth fairly sharp.

Puerto Rico: A mature female from Hucares (USNM 24460) has an abdomen as above but frontal teeth rather short and lobate, and anterolateral teeth short and not curved forward but with their anterior margin shorter than the posterior one. Another mature female (USNM 24457), from near Palo Seco, has its sixth abdominal segment shaped as in *C. maracaiboensis* (short, broad, rounded distally), short and rounded frontal teeth (mesial pair a bit sharper), and anterolateral teeth curved forward only in the lateral half of the row. A mature male from Cataño (USNM 24455) has anterolateral teeth short and not trending forward, first gonopods distorted in preservation but armed with spinules typical of *C. bocourti* (but a tip as in *maracaiboensis*), and short, lobulate frontal teeth (mutilated).

Trinidad: A mature female (USNM 137731) has the abdomen shaped as in *C. maracaiboensis*, and lobulate frontal and anterolateral teeth quite sharp and decidedly curved forward. Males in this lot have first gonopods typical of *bocourti* and anterolateral teeth moderately curved forward.

Venezuela: A mature female from Tacarigua de la Laguna, Estado Miranda (USNM 89644) has the sixth abdominal segment rounded distally and relatively short for its width, as in *C. maracaiboensis*, the mesial pair of frontal teeth moderately acute, lateral pair broader (both pairs fairly short), and sharply acuminate anterolateral teeth trending forward but not curved.

Costa Rica: A mature female (USNM 113279) has very lobate frontal teeth, erect anterolateral teeth strong and trending forward, and the sixth abdominal segment broken but rather indeterminate in shape (trending toward typical).

British Honduras: A mature female from near Belize (21377) has prominently lobulate frontal teeth, anterolateral teeth trending forward but sharp tipped only in the lateral half of the row, and the sixth abdominal segment halfway between the two extremes for the species (wide and broadly rounded distally).

Taissoun (1972) included some of these specimens in his comparative study. From this welter of conflicting trends, separation of *C. bocourti* from *maracaiboensis* was a weighted decision resting on characters prevalent in the Lago de Maracaibo populations plus environmental separation.

Distribution.—Jamaica and British Honduras to Estado de Santa Catarina, Brazil (Figure 27); extraterritorial occurrences in southern Florida and Mississippi, USA (both mature males).

Habitat.—*Callinectes bocourti* is associated with *C. sapidus* in many estuarine areas, but seems more tolerant of stagnant, polluted situations. Around the mouth of Lago de Maracaibo *C. bocourti* was found in the Golfo de Venezuela, Bahía de El Tablazo, Río Limón, and Estrecho de Maracaibo, but less abundantly in Lago de Maracaibo itself (Taissoun, 1969, 1972). Only adult females were found in the Golfo de Venezuela, but elsewhere both sexes in all stages of growth were common, abounding in Río Limón and mangroves around Puerto Caballo and in Bahía de El Tablazo, large males and juveniles being especially numerous around sewers of San Carlos and Punta de Palmas. Bottoms in this area vary from mud to sand. Griffiths, Cadima, and Rincón (1972) presented a similar account, showing that juveniles recruit to a fishery there in July and November, with mature males tending to remain in low-salinity water whereas females move to saltier water after mating. Coêlho (1967a) reported *C. bocourti* (called the blue crab there) abundant in a lagoon in Pernambuco that varies from 5‰ salinity in the rainy season to 29‰ in the dry season, and from other estuaries in northeastern Brazil (1970).

The broad range of tolerance is emphasized by presence in places such as a pool inside porous old coral rubble on Bonaire (Rathbun, 1936), and dark somewhat stagnant, polluted water at mouths of the Mero, Indian, and Salisbury Rivers on Dominica where sand bars blocked river flow at the time of investigation (Chace and Hobbs, 1969). Here the crabs actively fed on garbage in daytime over a bottom of rock-strewn sand covered with silt. In other streams on Dominica whose mouths were open to flow, only *C. sapidus* was found.

Spawning.—In all of the museum collections studied there are many containing mature females, but only five in which there are ovigerous specimens and only three of these are accurately dated: January, Puerto Rico, Panamá; February, Curaçao; November, São Francisco [Estado de Santa Catarina], Brazil. Taissoun (1969, 1972) found ovigerous females most abundant from March to August in the Golfo de Venezuela, and Griffiths et al. (1972) found them most abundant around the mouth of Lago de Maracaibo in July. These data suggest nearly year-round spawning (Taissoun, 1972) in one part or another of the range, perhaps with seasonal peaks associated with latitude.

Economic importance.—Holthuis (1959) described a fishery for *C. bocourti* in brackish waters of Surinam where it is the only portunid routinely caught, its tolerance of this habitat apparently favoring success there. The crabs are sold alive on the market in Paramaribo. A crab trap fishery around the mouth of Lago de Maracaibo started in 1969 and is increasing rapidly (Griffiths, et al., 1972). Though directed primarily at *C. sapidus*, a considerable number of *C. bocourti* are taken as well. Second half of the year is the season of highest catch per unit effort in a brackish area where males make up 90% of the take.

Remarks.—The collections examined contain an unusually large number of mature females.

The type series of *C. bocourti* in the MNHNP is somewhat confused by labels. No clear designation is given on labels of specimens which, by implication, can be associated with the original description. Two mature male specimens labelled "*Callinectes bocourti* A. M. Edw., Riviere de Mullins (12 m. NNW Stann Creek) au de Belize, Honduras, Coll. Bocourt" represent the types in the opinion of J. Forest. Identification, locality (excepting the parenthetic emendation), sex, and collector agree with Milne Edwards' description. The smaller specimen (size of carapace in mm: length 48, width at base of lateral spines 80, including lateral spines 90) has more granulate gastric, metagastric, cardiac, and branchial areas than the larger (length 60, width at base of lateral spines 102, including lateral spines 120). A small *Chelonibia* is affixed over the left epibranchial line on the anterolateral aspect of the mesobranchial area of the larger specimen. Both specimens lack right chelae, but have slender left minor hands with smooth rounded upper sides on the

propodus, that of the smaller specimen showing obsolescent granules; in both, the merus and carpus are smooth, with a very blunt outer spine on the carpus. The small specimen has a missing right third pereopod. In both, the first gonopods reach slightly beyond the telson.

Two male specimens labelled *"Callinectes cayennensis* A. M. Edw., Cayenne, Coll. Melinon" are possibly the types of *C. cayennensis*. Identification, locality, sex, and collector agree with Milne Edwards's description. Both dark in color, the specimens are obviously *C. bocourti*. The larger has only seven anterolateral teeth on the right side, the first tooth being enlarged. Both specimens have two apparent minor chelae, the larger of each smooth dorsally, and the smaller with obscurely granulate obsolescent ridges.

Finally, a dry male specimen labelled *"Callinectes bocourti* A. M. Edw., TYPE?, Honduras, Belize (Crust. Mexique, p. 226, 1881, Bocourt) A. Milne Edwards 1903" has a badly cracked carapace and bears the word "Belize" written obscurely in ink on the right mesobranchial eminence. The specimen, as shown by carapacic and pleopodal characters, is not *C. bocourti*, but rather *C. danae*, and was undoubtedly mislabelled subsequent to Milne Edwards's death in 1900, according to J. Forest. The broken abdomen exposes the tip of an intact first pleopod with tip turned ventrolaterally at the two-thirds level of sternite VI bearing a subterminal hair on the sternal aspect.

In the ANSP collection is a dry male specimen of *C. bocourti* (No. 2808 labelled *Lupa dicantha*) that is badly shrunken and distorted bearing the label "North America," but no date of collection nor indication of collector. The name and specimen suggest a collection made over a century ago representing a possible third record of the species from somewhere in the United States.

North American records may be explained by drift from the Caribbean, possible routes being suggested by drift bottle returns (Brucks, 1971).

Bott (1955) listed the species from the west rather than the east coast of Middle America by mistake.

Material.—Total: 117 lots, 290+ specimens.

Specimens listed in Rathbun (1930) from USNM (24459 not found) and MCZ, and in Holthuis (1959) from Surinam in RMNH.

USNM. 33 lots, 82 specimens, including the following not cited above:

PUERTO RICO

123085, 73279, Boca de Congrejos, 7 mi E San Juan, 31 Mar. 1937, 2 ♀, W. L. Schmitt. 77104, beach near Ponce, 17 Aug. 1932, 1 ♀, T. J. Barbour.

VIRGIN ISLANDS

St. Croix: 72354, Fairplain str. above bridge, 1935-36, 2 ♂, H. A. Beatty, No. 129. 76963, Altona str. 100 ft from sea, no date, 3 juv, H. A. Beatty, No. 199. 77100, Salt River reefs, no date, 17 juv, H. A. Beatty, No. 157.

BRITISH WEST INDIES

St. Lucia: 123086, Pigeon Island, 22 Mar. 1956, 3 ♂, 1 ♀, *Freelance*, Stn. 46-56.

COSTA RICA

113279, Limón Prov., Tortuguero R. about 2 mi above mouth at Leo's, 28 Apr. 1964, 1 ♀, 1 juv, D. P. Kelso.

COLOMBIA

78382, Puerto Colombia, no date, 1 ♀, Bro. Elias, No. 21.

VENEZUELA

89644, Estado Miranda, Tacarigua de la Laguna, 1 Mar. 1949, 1 ♀, Soc. Ciencias Nat. La Salle, Stn. c-3.

AHF. 1 lot, 1 specimen.

BRITISH WEST INDIES

Trinidad, West Manzanilla, 10°31′20″N, 61°02′37″W, 18 Apr. 1939, 1 ♂, *Velero III* Stn. A36-39.

AMNH. 4 lots, 4 specimens.

PUERTO RICO

2669, San Juan near San Antonio Bridge, 10 July 1914, 1 ♀, R. W. Miner. 5378, Culebra [18°18′N, 65°18′W], 1926, 1 ♂, H. E. Anthony.

BRITISH HONDURAS

Crique Salada [16°35′N, 88°37′W], Apr. 1951, 1 ♀, M. Gordon, Chable, and George.

PANAMA

11241, Harbor at Colón, no date, 1 ♀, *Arcturus* Exped.

ANSP. 3 lots, 9 specimens.

NORTH AMERICA [?]
2808. no date, 1 ♂ (dry).

[DOMINICAN REPUBLIC]
3519, Santo Domingo, no date, 2 ♀ (dry), W. M. Gabb.

PANAMA
1305, 5 ♂, 1 ♀, McNeil Exped.

BMNH. 9 lots, 12 specimens.

BRITISH WEST INDIES
1925.1.28.13, Tobago, 1 ♂, P. L. Guppy. 1938.3.29.18, Tobago, 1 ♂, A. K. Totton.

GUYANA
1960.10.5.15/16, Georgetown, Kitty Jetty, 1 ♂, 1 ♀, R. H. McConnell. 44.82, Georgetown, 1 ♂ (dry), vi/9. 62.93, 2 ♂, Leadbeater. 1949.5.26.1/2, 2 ♀, V. Graham.

SURINAM
1959.3.20.1, Suriname River near Paramaribo, 1 ♂, I. T. Sanderson.

BRAZIL
1923.8.14.1, Marajó I. mouth of Amazon, 1 ♂, Erhardt. 80.37, Pernambuco, 1 ♀, W. Forbes.

MCZ. 9 lots, 22 specimens, including the following not cited above:

PANAMA
5472, Aspinwall [= Colón], no date (recd. 13 Feb. 1861), 1 ♀, J. Rowell.

BRAZIL
5172, 13 Oct. 1873, 1 ♂ juv, C. Linden.

MNB. 2 lots, 3 specimens.

BRAZIL
Pernambuco: 329, Manques de Olinda, 1945, 2 ♂, Berla. Rio de Janeiro: 48, Maricá, no date, 1 ♀.

MNHNP. 2 lots, 4 specimens.

BRITISH HONDURAS
148, Rivière de Mullins au Sud de Belize, no date, 2 ♂, Bocourt.

FRENCH GUIANA
69, Cayenne, no date, 2 ♂, Melinon.

RMNH. 45 lots, 130+ specimens.

BRITISH WEST INDIES
Barbados: 23456, Holetown river pool, 18 Feb. 1964, 1 ♂, P. W. Hummelinck.

NETHERLANDS ANTILLES
Curaçao: 23450, N part Piscadera Baai, 25 Nov. 1963, 1 ♂, P. W. Hummelinck. 8122, Zaquito Lagoon, 1 Feb. 1949, 1 ♂, P. W. Hummelinck. 3270, Schottegat, 10 Feb. 1939, 1 ♀ (ov), H. S. C. Cossee. Schottegat near Pasanggrahan, 22 Aug. 1948, 1 ♀ (dry), P. W. Hummelinck. 11855 and 11858, slough in mangroves, Santa Cruz, 11 Feb. 1957, 2 ♂, 2 ♀, L. B. Holthuis, No. 1099. 11857, Waaigat, Willemstad, 30 Jan. 1957, many ♂♂ and juv, L. B. Holthuis.

Bonaire: Paloe Lechi, Apr. 1955, 1 juv (dry), J. S. Zaneveld. Paloe Lechi, Dralendijk, 5 Mar. 1957, 3 adult carapaces, (dry), L. B. Holthuis, No. 1137. 11856, Paloe Lechi, N Kralendijke, 5 Mar. 1957, ♂♂, ♀♀, and juv, L. B. Holthuis.

VENEZUELA
Estado Miranda: 7613, Laguna de Tacarigua, 1948-49, 2 ♀ (ov), G. Marcuzzi. Estado Sucre: 7615, beach by airfield, Cumaná, Sept. 1948, 1 ♀, G. Marcuzzi.

TRINIDAD
23403, Diego Martin R., 1965-66, 1 ♂, H. A. van Hagen.

SURINAM
21163, coast off mouth of Suriname and Coppename R., 25-27 Aug. 1964, 2 ♀, M. Boeseman. 21573, mouth of Suriname R. at Leonsberg near Paramaribo, 27 Dec. 1963, 1 ♂ juv, P. Leentvaar. 5367, Swamp near Agricultural Experiment Gardens, Paramaribo, 10 June 1941, 1 ♀ juv, D. C. Geijskes. 22495, brackish water at Matappica near Paramaribo, 6 Nov. 1965, ♂♂ and ♀♀, G. F. Mees. 22598, shore at Matappica near Paramaribo, 8-13 Jan. 1966, 1 ♂ and juv, G. F. Mees.

SADZ-B. 9 lots, 23 specimens.

BRAZIL
Maranhão: 876, 1919, 1 ♂, F. E. Sawyer, Smithsonian Inst. Alagoas: Lagoa Jequia Mangebeira Camargo, Nov. 1952, 3 ♂, 3 ♀. Bahia: 1248, Ilhéus, 1919, 2 ♀, E. Garbe. Rio de Janeiro: 1729,

Atafona, no date, 2 ♂, 2 ♀, Meneses. 3241 Atafona, 12 July 1963, 3 juv, N. Meneses. 399, Serra de Macaé, 1912, 2 ♂, E. Garbe. São Paulo: 400, Ubatuba, 1905, 1 ♀, E. Garbe. 403, Piassaquera, 1905, 3 ♂, J. S. Fialho. 352, Iquape, 1901, 1 ♂, R. Krone.

Gulf Coast Research Laboratory. 1 lot, 1 specimen.

UNITED STATES

Mississippi: 172:1062, Biloxi Back Bay, No., 1971, 1 ♂, from commercial fisherman (Perry, 1973).

Supplementary literature records.—Biscayne Bay, Fla. (Provenzano, 1961); St. Croix (Beatty, 1944); Dominica (Chace and Hobbs, 1969); Puerto Cortez, Honduras (Bott, 1955); Lake Maracaibo vicinity, Venezuela (Taissoun, 1969); Forteleza, Ceará, Brazil (Fausto Filho, 1966).

CALLINECTES RATHBUNAE CONTRERAS JAIBA PRIETA (MEXICO)

Figures 13, 19a, 20n, 22k, 27

Callinectes rathbunae Contreras, 1930, p. 238, text-figs. 9, 10 (type localities: Barras de Boca del Río, Buen País and Alvarado, Veracruz, Mexico).-Manrique Colchado, 1965, p. 30, figs. 10-15.-Taissoun, 1972, p. 35, figs. 1i-l, 2 (part), 3 (part), 9A, 10E-F, photos 8-11.

Callinectes rathbuni Pounds, 1961, p. 42, pl. 7, fig. 2d.

Description.—Carapace (Figure 13) bearing four acuminate frontal teeth with tips reaching a nearly common level, submesial teeth narrower and slightly shorter than laterals. Metagastric area with length and posterior width about equal, anterior width 2 times length. Anterolateral margins slightly arcuate, anterolateral teeth exclusive of outerorbital and lateral spine all acuminate with edges variably granulate, anterior margins of teeth a bit shorter than posterior margins, tendency to development of a shoulder on posterior margin of all except last tooth in row. Surface of carapace dorsally smooth and glistening around perimeter (when wet) and on epibranchial surfaces; central portion lightly and evenly granulate, cardiac area smooth anteriorly, granulate posteriorly. Epibranchial line prominent and sulci on central part of carapace deeply etched.

Chelipeds with sharply granulate ridges and usual spines; fingers of major chela heavily toothed but not gaping.

Male abdomen and telson long, extending nearly to juncture between thoracic sternites III and IV; telson lanceolate, much longer than broad; sixth segment of abdomen broadened distally. Mature female abdomen and telson reaching as far forward as in male, sixth segment nearly as long as fifth and with mesiodistal borders oblique, not markedly curved; telson elongate triangular with inflated sides. First gonopods of male (Figures 19a, 20n) reaching nearly to tip of telson beyond suture between sternites III and IV, overlapping in proximal half, diverging distally, twisting mesioventrally on axis lateral to abdominal locking tubercle on thoracic sternite V and recurving gradually to termination near midline; armed distally with a dorsolateral narrow band of large and small sharp retrogressive spinules. Gonopores of female (Figure 22k) ovate in outline with apex on long axis directed anteromesad; aperture of each sloping from surface along long mesial side under rounded, sinuous anterolateral border superior to prominent rounded eminence on posterolateral border.

Size of carapace in mm.—Largest male: length 61, width at base of lateral spines 107, including lateral spines 134. Largest female: length 66, width at base of lateral spines 116, including lateral spines 141. Summary of selected measurements taken from the small sample available is given in Tables 1 and 2. Manrique Colchado (1965) reported a male with length 62, width including lateral spines 144, and a female with length 62, width including lateral spines 150.

Color.—The only published descriptions of color are brief. Pounds's (1961) general account indicated that the colors are "clear shades of green and blue with tints of red, orange, and purple." Manrique Colchado (1965) characterized the carapace as obscure or dark green. Judging by greenish coloration of recently preserved specimens, both descriptions apply. Underparts are white.

Distribution.—Mouth of Rio Grande, Texas-Mexico border to southern Veracruz, Mexico (Figure 27).

Habitat.—Specimens available for study came from estuarine waters of ditches, lagoons, and river mouths, the type of environment reported by Manrique Colchado (1965) as coastal lagoons of varying salinity at depths of 1-3 m.

Spawning.—Although mature females are represented in the small study collection, none are ovigerous.

Remarks.—Apparently an isolate of *C. bocourti* stock confined to the western and southwestern Gulf of Mexico, *C. rathbunae* has various angularities on the body and legs more accentuated than in *C. bocourti*: 1) acute frontal spines contrasted with more rounded or lobate frontal spines (excepting juvenile *C. rathbunae* from Tamaulipas having rounded lobate frontals); 2) all anterolateral teeth acute (or acuminate) rather than anterior portion of series being rounded at tips; and 3) hand of chelae moderately ridged rather than smoothly rounded. First gonopods of mature male *C. rathbunae* are not crossed at the tips and fall a bit short of the telson tip whereas in mature *C. bocourti* they are crossed at the tips and slightly exceed the telson.

Specimens of neither species from Yucatán are available, thus areas of possible intergradation between seemingly close relatives have not been studied.

Material.—Total: 10 lots, 18 specimens.

USNM. 4 lots, 10 specimens.

MEXICO

Tamaulipas: 122925. Río Soto la Marina at Soto la Marina, 21 Jan. 1959, 1 ♀ (juv), R. R. Miller and R. J. Schultz, M59-1.

Veracruz: 122922, Laguna de Alvarado, 27 Apr. 1966, 1 ♂, 2 ♀, S. de la Campa, E. Ramírez and E. Chávez, L. B. 5093. 122923, Laguna de Pueblo Viejo off the corals, 4 Sept. 1964, 1 ♂, 1 ♀, J. A. Macías, L. B. 3333. 122924, Río Tuxpan, taken between Cobos and the Estero Quetumilco, 21 Nov. 1964, 2 ♂, 2 ♀, R. Márquez, L. B. 3632.

A ♂ with carapace 30 mm long collected from Rio Grande by Trevino and sent to USNM for identification by H. Hildebrand, 4 Sept. 1956; identified by F. A. Chace, Jr., and returned to sender.

AHF. 2 lots, 3 specimens.

MEXICO

Veracruz: Boca del Río, seined in shallow water, 9 Aug. 1949, 1 ♂, 1 ♀, B. W. Halstead. Drainage ditch 5 mi W Veracruz, seined in brackish water, 19 Aug. 1949, 1 ♀ (juv), B. W. Halstead.

BMNH. 1 lot, 1 specimen.

MEXICO

65.29, 1 ♀, (dry), vi/7.

RMNH. 1 lot, 2 specimens.

MEXICO

Veracruz: 21814, Laguna de Pueblo Viejo, 25 Apr. 1964, 1 ♂, 1 ♀, F. A. Manrique Colchado.

Instituto Nacional de Investigaciones Biológico Pesqueras, Mexico, D. F. 2 lots, 2 specimens.

Tamaulipas: Laguna del Chairel y río Tamesí, 18 Aug. 1964, 1 ♂, J. A. Macías. Veracruz: Estero Jacome, 18 Dec. 1963, 1 ♀ (juv), S. García.

Supplementary literature record.—Mouth of Rio Grande, Tex. (Pounds, 1961).

CALLINECTES MARACAIBOENSIS TAISSOUN

Figures 14, 19b, 20o, 22l, 27

Callinectes sp., Taissoun, 1969, p. 63, fig. 23, photo 8.

Callinectes maracaiboensis Taissoun, 1962, p. 12, 23, figs. 1e-h, 2 (part), 3 (part), 4, 9B, 10A-B; photos 1-2 (col.), 3, 4m (type: ♂, Museo de Ciencias Naturales, Caracas, Venezuela, Lago de Maracaibo, Venezuela).- 1973, p. 28, figs. 4F, 5E, photo 3.

Description.—Carapace (Figure 14) bearing four triangular frontal teeth with tips meeting a nearly common level, lateral pair moderately acute with mesial side having a flatter angle than lateral side, submesial pair much narrower, acute, sometimes slightly shorter than lateral pair. Metagastric area with length and posterior width about equal, anterior width 2 times length. Anterolateral margins slightly arcuate, teeth exclusive of outer orbital and lateral spine with tips directed outward, tending to be acuminate especially in outer portion of row, posterior margin of teeth usually longer than and more granulate

than anterior margin. Surface of carapace dorsally smooth and glistening around perimeter (when wet) and on epibranchial and posterolateral surfaces; granules scattered on epibranchial surfaces, progressively more crowded on proto-, meso-, and anterior portion of metagastric areas and branchial lobes and on cardiac area (especially posterior slope). Epibranchial line prominent and relatively uninterrupted, sulci on central part of carapace deeply etched.

Chelipeds granulate on ridges, fingers of major chela heavily toothed, lower margin of propodal finger often decurved near base in adults.

Male abdomen and telson long, extending to anterior quarter of thoracic sternite IV; telson lanceolate, much longer than broad; sixth segment of abdomen broadened distally. Mature female abdomen and telson reaching at least as far forward as in male, nearly to juncture between thoracic sternites III and IV, sixth segment as long as fifth and fully rounded at its distolateral corners, telson elongate-triangular with sides slightly inflated. First gonopods of male (Figures 19b, 20o) very long, often extending nearly to tip of telson and crossed near tips; sinuously curved and overlapping in two places proximally, diverging distally, twisting mesioventrally on axis lateral to abdominal locking tubercles on thoracic sternite V, and recurving gradually to termination near midline; armed distally with a dorsolateral band of large and small retrogressive spinules. Gonopores of female (Figure 22l) asymmetrically ovate in outline with apex on long axis directed anteromesad; aperture of each sloping from surface on mesial side under rounded sinuous anterolateral border superior to rounded lateral and much smaller mesial eminences on posterior border.

Size of carapace in mm.—Largest male available: length 78, width at base of lateral spine 134, including lateral spines 159. Largest female available: length 58, width at base of lateral spines 102, including lateral spines 124. Taissoun (1972) measured large samples made up of individuals whose mean sizes were comparable to the above specimens, males generally being larger than females. Summary of selected measurements for the few specimens available is given in Tables 1 and 2.

The following account is from Taissoun (1972), the only person who has studied the species in detail.

Color.—Adult male: carapace olive green with tints of light brown and blue toward central region, anterolateral region with light chestnut areas. Chelipeds with upper portion light chestnut and olive green with orange tints; distal portions of merus, internal portion of carpus, internal and external sides of fingers intense blue; spines of merus brownish orange distally with tips light chestnut and cream, bases obscure brown; distal tubercles on propodus orange and intense blue. Ambulatory legs cream proximally, blue distally, articulations with tubercles intense orange. Swimming legs intense blue and cream dorsally, terminal article blue, obscure brown and light orange, tubercles orange. Underparts cream and light yellow, except anterior portion and pereopods light blue.

Females: as males but with more intense blue on internal part of chelipeds. Taissoun (1972) included colored illustrations, but the female pictured is more reddish than as described above.

Variation.—Granulation of the carapace varies from nearly smooth to fairly marked, but is not so prominent as in some specimens of *C. bocourti*. Lateral spines of males are occasionally curved forward at the tips, but in females are often relatively longer and straighter. Meral spines on the chelipeds vary in number as usual in the genus (four or five) and all spines become worn in old individuals.

Distribution.—Confined to the Lago de Maracaibo estuarine system, roughly 120 km wide × 215 km long, extending from Bahía del Tablazo emptying into Golfo de Venezuela in north, through Estrecho de Maracaibo southward into Lake proper.

Habitat.—The species occurs on sandy and muddy bottoms, and among roots of mangroves, in brackish to occasionally fresh waters containing much silt and decomposing organic material. Both *C. maracaiboensis* and *bocourti* occur in the Lake and its outlet, apparently most abundantly near the mouth where all developmental stages of both are found, but the majority of these are adult males in salinities ranging from 0.35 to 15.12‰. Surface temperatures in the Lake are fairly uniform, ranging from 27.2° to 32°C, and undergoing a diurnal change of ± 1°C, but below depths of 10 m temperature remains even more uniform. Tem-

perature of surface water in the Golfo de Venezuela is less than in the Lake (28.6°C in October and 25.9°C in February were recorded by Taissoun (1972)).

Spawning.—Adaptation to the Lake environment is shown by spawning habits. Ovigerous *C. maracaiboensis* were occasionally taken in Bahía del Tablazo and Estrecho de Maracaibo from April to August where salinity ranged from 3.15 to 15.13‰. Ovigerous female *C. bocourti* were usually found in the Golfo de Venezuela where salinity varied between 23.9 and 34.6‰, and only occasionally in the fresher Bahía del Tablazo.

Economic importance.—A developing fishery in the Lago de Maracaibo region employing crab traps concentrates chiefly on *C. sapidus*, but includes *C. maracaiboensis* and *C. bocourti*.

Remarks.—Recognition of this new species from a restricted geographic range comes as some surprise in view of the broader distribution of other members of the genus. There is no doubt that *C. bocourti, maracaiboensis,* and *rathbunae* are very closely related, the widely ranging *bocourti* probably being the parent stock from which the isolates in peripheral areas have evolved. *Callinectes maracaiboensis* and *rathbunae* are similar in having somewhat less robust bodies than *bocourti,* smaller, sharper, outwardly directed anterolateral teeth and, in adults, more acuminate frontal teeth. In this regard, Taissoun's (1972:10) outlined median saggital sections of the three species do not seem to represent the average. Shape of abdomen in adult females is another useful character, that of *C. maracaiboensis* being somewhat smaller, having a sixth segment short and evenly rounded on the distal edge, but narrower than in *rathbunae.* Typically mature *C. bocourti* females have a relatively smaller abdomen than either of the others, with the distal edge of the sixth segment being somewhat angular distolaterally rather than broadly rounded.

Taissoun (1972) marshalled evidence for estuarine adaptations in *C. maracaiboensis,* which apparently parallels similar trends in engraulid fishes, the whole process presumably being associated with isolation of the Lake accompanying fall in sea level during the Pleistocene. The habitat of this species suggests interesting comparative experiments on larval development of a form adapted to living in lowered salinity throughout life as contrasted with the other more catadromous species of the genus.

Material.—Total: 4 lots, 16 specimens.

USNM

VENEZUELA

139621, Lago de Maracaibo, 19 July 1970, 1 ♂, 1 ♀ (Paratypes), E. Taissoun. 143392, Lago de Maracaibo, no date, 5 ♂, 1 ♀, E. Taissoun. 143391, Lago de Maracaibo, 23 June 1972, 5 ♂, 1 ♀, E. Taissoun. 143393 Puerto Caballo, Maracaibo, Lago de Maracaibo, 17 June 1968, 1 ♂, 1 ♀, E. Taissoun.

CALLINECTES LATIMANUS RATHBUN

Figures 15, 19c, 20p, 23a, 27

Callinectes bocourti.- Rathbun, 1896, p. 362 (part), fide Rathbun, 1921.- 1897, p. 151 (part), fide Rathbun, 1921.- 1900a, p. 290.- Balss, 1921, p. 58.

Callinectes latimanus Rathbun, 1897, p. 151, text-figs. 6-8 (syntypes: 4 ♂, 3 ♀, BMNH 91.4.1.63/69; 1 ♂, USNM 19877; Lagos, Bight of Benin, Guinea [Nigeria], A. Moloney).- 1900a, p. 291.- 1921, p. 398, text-fig. 4, pl. XV, fig. 2, pl. XXI, pl. XXII, fig. 1.- Odhner, 1923, p. 22.- Monod, 1927, p. 606.- 1956, p. 211, figs. 240- 243.- Irvine, 1947, p. 297, fig. 202 [?].- Vilela, 1949, p. 58.- Capart, 1951, p. 132, fig. 47.- Rossignol, 1957, p. 82.- 1962, p. 116.- Forest and Guinot, 1966, p. 65.

Neptunus marginatus var. *truncata* Aurivillius, 1898, p. 5, pl. 1, figs. 1-4 (type: 1 immature ♀ [not ♂], fide Rathbun, 1921, Cameroon).

Callinectes diacanthus var. *africanus*.- A. Milne Edwards and Bouvier, 1900, p. 71 (not col. pl. 4, fig. 5 = *C. sapidus*).- Lenz, 1910, p. 125 [5].- Gruvel, 1912, p. 3, 6, pl. 2, fig. 1.

Callinectes marginatus.- Odhner, 1923, p. 21.

Callanectes Sp. (?).- Irvine, 1932, p. 14, fig. 13.

Description.—Carapace (Figure 15) bearing four frontal teeth with variably rounded tips, submesial pair shorter than lateral pair. Metagastric area with length approximately equal to posterior width, anterior width about 2 times length. Anterolateral margins moderately

arched, anterolateral teeth exclusive of outer orbital and lateral spine varying from acute with serrate margins to increasingly acuminate and forward curving with nearly smooth margins at lateral end of row. Lateral spine relatively stout. Surface of carapace coarsely granulate, but granules more widely spaced or absent near margins, on epibranchial surfaces, and along regional sulci; most closely crowded granules on mesogastric, cardiac, and mesobranchial areas. Epibranchial line prominent and nearly uninterrupted.

Chelipeds with propodus and carpus moderately ridged, granules on dorsal and lateral ridges becoming smooth with age; chelae of large specimens very strong, major one often very broad with fingers heavily toothed (if not worn), lower margin of propodal finger often decurved near base opposite enlarged basal tooth of dactylus.

Male abdomen and telson reaching beyond midlength of thoracic sternite IV; telson lanceolate, much longer than broad; sixth segment of abdomen broadened distally. Mature female abdomen and telson reaching about midlength of thoracic sternite IV; telson elongate triangular with inflated sides, sixth segment longer than fifth. First gonopods of male (Figures 19c, 20p) very long, usually exceeding telson and crossed near tips; sinuously curved and overlapping proximally, diverging distally, twisting mesioventrally on axis lateral to abdominal locking tubercle and recurving to termination near midline; armed distally with dorsolateral band of large and small retrogressive spinules. Gonopores of female (Figure 23a) ovate in outline with apex on long axis directed anteromesad; aperture of each sloping from surface on mesial side under rounded, sinuous anterolateral border superior to a rounded eminence on posterior border.

Size of carapace in mm.—Largest male: length 71, width at base of lateral spines 125, including lateral spines 151. Largest female: length 59, width at base of lateral spines 105, including lateral spines 127. Summary of selected measurements is given in Tables 1 and 2. The species is characteristically large at adult size, Irvine (1947) reporting carapace widths of 8-12 inches (20-30 cm).

Color.—Uniform greenish brown with articulations and internal face of chela and dactyl bluish; ventral aspect yellowish white (Rossignol, 1957). Khaki colored with bluish tinge and bluish legs (Irvine, 1932, 1947); predominantly brown, perhaps where waters are often turbid with silt (Longhurst, 1958). A mottled olive coloration persists at least as long as 20 yr in some preserved specimens.

Variation.—Aptly named for one of their most distinctive features, adults of *C. latimanus* have broad major chelae. Chelae with worn tooth rows and gaping fingers seem disproportionately large in old males, and in their smooth surfaces these may resemble the hands of *C. bocourti* (excellent example, AMNH 3111), but the entire cheliped is shorter and thicker than in that species. There is usually a strongly developed proximal tooth on the dactyl of the major hand and opposite it a strongly decurved propodal finger. The minor chela (normally left) is much slimmer than the major, its two fingers toothed with meshing sectorial triads or variants of this pattern.

Especially in juveniles, the submesial pair of frontal teeth often overhangs and obscures the epistomial tooth, though not so completely as in *C. toxotes*. Adult females have coarse granulations over the whole carapace though not so closely crowded at the edges as in central elevated parts behind the epibranchial line. There are smooth areas between more scattered granules in front of the epibranchial line in both sexes.

First gonopods of males may extend beyond the telson.

Distribution.—Baie de Saint-Jean [19°27′N, 16°22′W], Mauritania, to Cabinda, Angola (Figure 27). (Perhaps farther south in Angola on basis of published accounts such as Gruvel [1912] and Monod [1956], and specimens of uncertain origin [AMNH 5895].)

Habitat.—In a category Longhurst (1958) called "mobile invertebrates," the most important estuarine species in the Sierra Leone River (site studied) appeared to be *C. latimanus* and *Parapenaeopsis atlantica* Balss. Neither of these was completely restricted to the estuary but occurred only sporadically outside it. *Callinectes latimanus* was most abundant in the midestuarine region in many of the otter-trawl hauls, and extended far up creeks to low-salinity water. Sourie (1954b) found *C. latimanus* widely distributed in estuaries of Senegal ranging from fresh water to salt concentrations near saturation, and Gruvel (1912) reported brackish water habitats in

Ghana where the species abounds on muddy bottoms. Crosnier (1964, and pers. data) and a number of others listed the depth range as 0-35 m in warm water.

Callinectes latimanus is preyed upon by *Galeoides decadactylus* Bloch and *Pomadasys jubelini* Cuvier (Longhurst, 1957), and *Callinectes* sp. [probably *latimanus*] by *Dasyatus margarita* Gunther and *Caranx alexandrinus* Cuvier and Valenciennes (Monod,.1927).

Spawning.—In all museum material available to me only four collections that are dated contain ovigerous females: January-February, Ivory Coast; May, Senegal, Nigeria; October, Togo. In the warm West African region it is likely that spawning occurs the year round, but may be concentrated at seasonal peaks.

Economic importance.—There is no literature on strictly commercial aspects of a fishery for this species, but it is important as food in coastal communities. Rathbun (1900a) recounted an early report that the crab was found only in fresh water of rivers, and much sought after for the exceptionally good meat. Monod (1927) listed *C. latimanus* as common in the Cameroons and customarily eaten there. Gruvel (1912) wrote that it is extremely abundant along the coast from Senegal to Angola, and so much so in certain areas such as the Ivory Coast, Dahomey, etc., that the people there brought large basketfulls alive to the markets to be either boiled in water or fried in palm oil. He regarded the crabs as extremely tasty and therefore subjects for a fishery, at least from Senegal to the Cameroons, where they were captured around lagoons and among mangroves in brackish water, generally on mud bottom, by means of small seines, baited traps, or fishing lines. Irvine (1947) listed similar fishing methods and considered the crabs quite edible, while Rossignol (1957, 1962) considered this crab the most abundant in the genus, subject to a regular fishery by native peoples in estuaries and lagoons, and although acceptable, not always so savory as *Portunus validus* Herklots.

Remarks.—The syntype male in the USNM (19877) is a mature specimen with first gonopods extending beyond the telson, a quite sharply granulate carapace with acute anterolateral teeth (especially from the fourth tooth laterad), and a left chela with strong proximal tooth on the dactyl heavier than the right, but it is a poor specimen because both chelipeds are detached from the body and parts of other legs are detached or missing. The series of syntypes in the BMNH (91.4.1.63/69) is in much better condition, consisting of two mature and two immature males, and one mature and two immature females. The largest male is the most perfect specimen, and the first gonopods on it exceed the tip of the telson.

The early confusion of this species with the American *C. bocourti* is easy to understand because each is described comparatively in terms of the other, the relationships being obviously close.

Material.—Total: 39 lots, 116 specimens.

USNM. 9 lots, 16 specimens.

SENEGAL
18735, no date, 1 ♂ juv, from Mus. Nat. Hist., Paris.

LIBERIA
123087, Robertsport, Grand Cape Mount Co., 28 Dec. 1947, 1 ♀, J. T. Baldwin, Jr.

NIGERIA
120943, Lagos, 06°28′N, 03°23′E, 10 May 1965, 1 ♀, *Pillsbury*. Lagos, Guinea [= Nigeria], nodate, 1 ♂, A. Molony, (Type).

ANNOBÓN ISLAND
120944, 01°24′S, 05°37′E, 20 May 1965, 2 ♂, 2 juv, *Pillsbury*, Stn. 281.

ZAIRE
54253, 54254, 54310, Banana, mouth of Congo River, July-Aug. 1915, 5 ♂, 2 ♀, H. Lang.

AMNH. 6 lots, 15 specimens.

ZAIRE
3326, no date, 1 ♂, Congo Exped. 3110, 3111, 3112, 3417, Banana, July-Aug. 1915, 7 ♂ (1 dry), 4 ♀ (1 juv), H. Lang and J. Chapin.

ANGOLA [?]
5895, 1925, 2 ♀, Vernay Angola Exped.

BMNH. 6 lots, 17 specimens.

SIERRA LEONE
1916.6.23.1/2, Gbanbama, 1 ♂, 1 ♀, N. W. Thomas. 1922.9.13.6/7, Sherbo I., 2 ♀, C. H. Allan.

GHANA
Accra, no date, 1 ♂, 1 ♀, F. R. Irvine.

NIGERIA
91.4.1.63/69, Lagos, Bight of Benin, 4 ♂, 3 ♀ (2 juv), A. Moloney, (Types). 1948.4.30.1/2, Lekki Lagoon, 16.2.1947, 2 ♂, Trewavas.

ANGOLA
1912.4.2.4/5, Chiloango River, Cabinda, July 1911, 2 ♂, Ansorge.

MNHNP. 5 lots, 7 specimens.

GAMBIA
Basse, Côte de Troire, 1907, 1 ♂, Bouet.

SENEGAL
No number, 1 ♂, 1 ♀ juv, date and col. unknown. Bignona, May 1946, 2 ♂, P. L. De Keyser and A. Villiers.

GUINEA
Conakry, Guinée, 1 ♀, Inst. Fr. d'Afrique Noire.

CONGO
1892-94, 1 ♂ juv, Dybowski.

RMNH. 6 lots, 20 specimens.

LIBERIA
Grand Cape Mount, 1881, 1 ♂, J. Büttikofer and J. A. Sala. 1864, Fishermans Lake, [35 mi NW Monrovia], among stones, Jan. 1881, juv 2 ♂, 2 ♀, J. Büttikofer and J. A. Sala.

GHANA
376, St. George d'Elmina, 1 ♂, H. S. Pel.

NIGERIA
20614, Lagos harbor, 23 May 1964, 1 ♀ (ov), *Pillsbury*. 15533, Niger Delta, May-Aug. 1960, 3 ♂, 3 ♀, H. J. G. Beets.

CONGO
No number, 1880, (juv) 2 ♂, 5 ♀, T. Kamerman.

UNC-IMS. 7 lots, 41 specimens, from A. Crosnier.

TOGO
2733, Lagune D'Anecho, 5 ♂, 3 ♀, A. Stauch. 2734, Côtes du Togo, 06°06′30″N, 01°37′30″E, 16 Oct. 1963, 1 ♀ (ov), A. Crosnier.

CAMEROON
2735, Cotes du Cameroun, 03°34′N, 09°35′E, 23 Aug. 1963, 1 ♀, A. Crosnier.

CONGO
2736, Lagune de Zambi [03°58′S, 11°17′E], 13 May, 1964, 2 ♀, A. Stauch. 2737, Lagune de Conkouati [03°58′S, 11°19′E], 14 May 1964, 1 ♀, 17 juv, A. Stauch. 2738, Plage de Pointe-Noire, no date, 2 ♂, 2 ♀. A. Crosnier. 2739, Plage de Pointe-Noire, July 1963, 4 ♂, 4 ♀, A. Crosnier.

Supplementary literature records.—Baie de Saint-Jean [19°27′N, 16°22′W], Mauritania; St. Louis, Yof, Sobané [= Sobène?], Bignona, Sédhiou + 3 nearby localities, Ziguinchor, Senegal; Tamara, Ile Poulet, Guinea; Abidjan, Lagune Ébrié, Baie de Cocody, Ivory Coast; near Densu, Gold Coast [= Ghana] (Monod, 1956); Bissau, porto de Biombo, Ilhéu de Âncora, Portuguese Guinea (Vilela, 1949); Sierra Leone River (Longhurst, 1958); Gold Coast (Irvine, 1947); Fernando Póo (Crosnier, 1964); Príncipe I. (Forest and Guinot, 1966); Senaga, Cameroon (Odhner, 1923); Songolo [= Songololo], Loya, Longo, Djeno, Congo (Rossignol, 1957).

CALLINECTES SAPIDUS RATHBUN
Blue Crab

Figures 1, 16, 17, 19d, 21, 23b-c, 26

Portunus hastatus.- Bosc, 1802, p. 212-214,219.- 1830, p. 234.

Lupa hastata.- Say, 1817, p. 65 (not *L. hastata* Desmarest, 1832 = *Cancer hastatus* Linnaeus, 1767).

Portunus diacantha Latreille, 1825, p. 190 (variety) (type localities: North America, Antilles, Brazil, etc.; types not extant; restricted to Philadelphia, Pa., by Holthuis, 1962, p. 232; name suppressed by International Commission of Zoological Nomenclature, Opinion 712 [1964, p. 336]).

?*Lupea dicantha*.- H. Milne Edwards, 1834, p. 451 (part).

Lupa dicantha.- Gould, 1841, p. 324.- de Kay, 1844, p. 10, pl. 3, fig. 3.- Holmes, 1858, p. 9 (fossil).

Callinectes diacanthus.- Stimpson, 1860, p. 220.- Young, 1900, p. 186 (part).

Callinectes hastatus.- Ordway, 1863, p. 568 [3].- A. Milne Edwards, 1879, p. 224 (var. of *C.*

diacanthus).- R. Rathbun, 1884, 1893, p. 775, pl. 267.- Young, 1900, p. 187 (var. of *C. diacanthus*).

?*Neptunus hastatus*.- Brocchi, 1875, p. 55, pl. 16, fig. 81.

Neptunus (Callinectes) diacanthus.- Ortmann, 1894, p. 77 (part: specimens g, Florida; l, Brazil; n, Haiti).

Callinectes sapidus Rathbun, 1896, p. 352, pl. 12; pl. 24, fig. 1; pl. 25, fig. 1; pl. 26, fig. 1; pl. 27, fig. 1 (type locality restricted to "east coast of United States" by Williams, 1965).- 1929, p. 31, fig. 41.- 1930, p. 99, text-figs. 15a, 16c, 17c, 18a, 19, pl. 47.- Bouvier, 1901, p. 16.- Clark, 1906, p. 172, pl. 41, figs. 1-3 (fossil).- Verrill, 1908a, p. 370, text-figs. 22a, 23a, 24, pl. 17, fig. 2.- Hay and Shore, 1918, p. 432, pl. 35, fig. 1.- Chace, 1940, p. 33.- Chace and Hobbs, 1969, p. 133, figs. 36, 37f.- Balss, 1957, p. 1641.- Holthuis, 1961, p. 50, pl. 1, fig. 2, pl. 2, fig. 2.- 1969, p. 34, pl. 1.- Holthuis and Gottlieb, 1955, p. 91, pl. 3, fig. 11.- Pounds, 1961, p. 42, unnumbered col. frontis., unnumbered text-fig. p. 9, text-figs. 1-2, pl. 7, figs. 1, 2a.- Futch, 1965, p. 2, figs. 1, 2, 3, 4, 5c.- Williams, 1965, p. 168, fig. 151.- Christiansen, 1969, p. 72, fig. 29.- Taissoun, 1969, p. 37, photos 3-6, figs. 11A-D.- 1973, p. 34, figs. 4E, 5F, photo 5.

Callinectes sapidus acutidens Rathbun, 1896, p. 354, pl. 13; pl. 24, fig. 2 (type: ♂, MCZ 4696, Santa Cruz [Estado de Bahia] Brazil, Thayer Exped.).-1901, p. 47.- 1930, p. 111, text-fig. 15 c, pl. 48.- 1933, p. 48.- Young, 1900, p. 191.- Contreras, 1930, p. 228, fig. 1.- Pretzmann, 1966, p. 305, 2 pls.- Bulgurkov, 1968, fig. 1.

Callinectes africanus.- A. Milne Edwards and Bouvier, 1900, pl. 4, fig. 5 (not p. 71, var. of *C. diacanthus* = *C. marginatus*).

Description.—Carapace (Figures 16, 17) bearing two broad either obtuse or acuminate, triangular frontal teeth with mesial slopes (incorporating a pair of rudimentary submesial teeth) longer than lateral slopes. Metagastric area with posterior width approximately 1.2 times length, anterior width about 2 times length. Anterolateral margins slightly arched; anterolateral teeth exclusive of outer orbital and lateral spine obtuse to acuminate and directed outward more than forward. Much of surface smooth, with scattered granules, but granules concentrated locally on mesobranchial, posterior slope of cardiac, and anterior portion of mesogastric area; a tendency to crowding of granules into transverse ridge at summit of cardiac and mesobranchial area in some individuals. Sculpturing of surface varying individually from low to raised relief. Lateral spines varying from rather stout, blunt, and forward trending to slender, elongate, and slightly backward trending. Epibranchial line nearly straight over branchial region, otherwise sinuously curved.

Propodus and carpus of chelipeds with moderate finely granulate ridges, width of chelae similar, propodal finger of major hand occasionally with lower margin decurved proximally.

Male abdomen and telson reaching about midlength of thoracic sternite IV; telson lanceolate, much longer than broad; sixth segment of abdomen broadened distally. Mature female abdomen and telson reaching about midlength of thoracic sternite IV; telson with inflated sides almost equilaterally triangular, fifth and sixth abdominal segments equal in length. First gonopods of male (Figures 19d, 21) very long, reaching beyond suture between thoracic sternites IV and V but not exceeding telson; sinuously curved and overlapping proximally, diverging distally, twisting mesioventrally on axis lateral to abdominal locking tubercle and recurving to termination near midline; armed distally with row of large and small retrogressive spinules following ventral and lateral borders with twist of axis; tip membranous, flared portion suggesting an elongate quadrilateral in outline. Gonopores of female (Figure 23b, c) paraboloid in outline with apex on long axis directed anteromesad, aperture of each sloping from surface on mesial side under irregularly rounded and linearly wrinkled anterior border superior to bulbous posterolateral border.

Size of carapace in mm.—Largest male: length 91, width at base of lateral spines 168, including lateral spines 209. Largest female: length 75, width at base of lateral spines 143, including lateral spines 204. Mature size of females varies considerably, the smallest examined having a carapace length of 21, width at base of lateral spines 41, including lateral spines 55. Summary of selected measurements is given in Tables 1 and 2.

Pretzmann (1966) discussed a large immature female with acute spines: length 65, width 132.5. The largest immature female I have seen, also with fairly acute spines, reached a carapace

length of 60, width at base of lateral spines 109, including lateral spines 135. Some others in material studied approached this size. All such specimens seen by me are from the Gulf of Mexico and may represent parasitized individuals in which the maturation process has been altered.

Color.—Grayish, bluish, or brownish green of varying shades and tints dorsally on carapace and chelipeds; spines may have reddish tints, tubercles at articulations of legs orange, and legs varyingly blue and white with traces of red or brownish green. Males with propodi of chelae blue on inner and outer surfaces, fingers blue on inner and white on outer surfaces and tipped with red. Mature females with orange fingers on chelae tipped with purple. Underparts off-white with tints of yellow and pink. Futch (1965) and Taissoun (1969) gave a good description of color; De Kay (1844), Milne Edwards and Bouvier (1900; plate IV, Figure 5), Churchill (1919), and Pounds (1961) published colored illustrations of the species, and still others are scattered in popular literature.

Color variations other than those associated with sexual dimorphism and molt cycle are known. Albinos or partial albinos are in museum collections and have been reported both in systematic literature and elsewhere (Gowanloch, 1952; Sims and Joyce, 1966). Haefner (1961) reported an adult male lacking dorsal green coloration and bright blue and scarlet markings on the legs. Instead, the upper surface of the carapace was "robins egg blue" and the appendages were paler than usual, but the abdomen and underparts had normal color. A similar blue specimen was reported elsewhere (Maryland Tidewater News, 1950). Haefner also pictured a bilateral gray and brown colored specimen from the collection of L. Eugene Cronin. Hopkins (1962, 1963) discussed biochemistry of the sexual color dimorphism.

Variation.—There are morphological variations in this species having far greater systematic interest than size and color. Study of many specimens from throughout the range of the species bears out the conclusion of Chace and Hobbs (1969) that extreme variants "are so different from each other that they could easily be interpreted as distinct species," but there is "no point of demarcation"—morphological, geographic, bathymetric—between the "typical" rather blunt-spined form predominating along the east coast of the United States and the acute-spined form named *C. sapidus acutidens* by Rathbun predominating from Florida southward.

Rathbun (1896) characterized the "acutidens" form (paraphrasing) as being wider than the "typical" with all prominences more strongly marked, areolations separated by deeper depressions, granules more raised, gastric ridges stronger and more sinuous, a transverse granulate ridge on each cardiac lobe, frontal teeth narrower and more acute and bearing two small intervening teeth, anterolateral teeth broad at base and narrowing abruptly to long acuminate tips with margins granulate, lateral spines longer than in "typical" specimens of equal size, and ridges of chelipeds quite prominent and strongly granulate. Figures 16 and 17 show two extremes, the first a mature young male of typical form, and the second a mature male of "acutidens" form.

I thought for a time that a species distributed through approximately 85° of latitude from North Temperate through Tropic to South Temperate Zones might reflect responses to temperature in spination or other characters, "typical" structure being prevalent in the temperate zones and sharp spination in the tropics, the differences thereby justifying nomenclatural recognition. There is weak but inconsistent evidence for this pattern. Though "acutidens" individuals are uncommon outside the tropics, intermediates occur everywhere to some degree, and some "typical" individuals occur in the tropics. Genetic pooling or environmental response reflected in morphology seems poorly structured.

For example: Occasional specimens found as far north as Woods Hole, Mass., (USNM 4946, 40723, 43178) are nearly as sharp spined as some Caribbean material. Churchill (1919, plates 53-54) pictured individuals from Chesapeake Bay that approach the "acutidens" form. In the collection of the USNM is a huge male from Wye River, Md., (92452) that has acuminate anterolateral and suborbital teeth, though not so attenuated as in Florida material; two carapaces from Virginia (76184) have such acute spines that Rathbun identified them as the "acutidens" form; and a huge lot (60601) from Hatteras, N.C., composed of mainly "typical" blunt-spined individuals characteristic of eastern United States shows variation in frontal teeth from no submesial frontals to rudimentary evidence for their presence. In Maryland, few specimens examined show easily identifiable submesial teeth on the inner

slopes of the prominent frontal teeth, but in material from Louisiana there is a tendency to development of the submesial frontals, and the anterolateral teeth are generally more acute than in Chesapeake Bay material. Specimens from Veracruz, Mexico, in the AHF collection show rather blunt frontal but acuminate anterolateral teeth and rather prominent regions on the carapace. Most specimens from southern Florida to southern Brazil approach the "acutidens" form, but throughout this vast region there is much variation.

The sharpest- and longest-spined forms with most prominent development of rudimentary submesial frontal teeth occur in the western Caribbean Sea along the Guatemala-Panama coast. These individuals also have regions on the carapace more deeply and sharply sculptured than in the "typical" form, sharp granulation on both carapace and chelipeds, and cardiac and to some extent mesobranchial regions exhibiting a crowding of granules at the apex leading to formation of slight transverse ridges, but with the anterior slopes of these regions lacking granules. While some specimens from Puerto Rico approach those from the western Caribbean in ornamentation, there is a mixture of "typical" features in many individuals, as elsewhere in the Antilles. Perhaps the best illustration of mingling features is illustrated by three lots of specimens in the RMNH. In 23404 from Trinidad are two males. Both have crowding of granules into a transverse ridge on the cardiac lobes with largest granules behind and fewer on the anterior slope, and a faint tendency to ridging of granules on the mesobranchial regions. The smaller specimen has the more deeply sculptured carapace, but rather blunt frontal, outer orbital, and suborbital teeth, and rather short, acute anterolateral teeth except for the last two which are acuminate. The larger specimen has a rather smooth carapace, but acuminate, long, and outwardly turned outer orbital and suborbital teeth, rather acute frontals with rudimentary submesial teeth, and quite acuminate anterolateral teeth throughout the length of the row. Another male from Trinidad (17738) has a transverse row of crowded granules on each cardiac lobe with the anterior slope relatively smooth, and mesobranchial regions with crowded granules but no ridging. The frontal teeth are neither especially sharp nor sinuous mesially, and the anterolateral, outer orbital, and suborbital teeth, like many "typical" specimens, are acuminate but not markedly so. Two females from Curacao (11881) seem to be nearly "typical" in all respects. One of them has granules crowded into a poorly defined transverse ridge on each cardiac lobe; however, there are granules on the anterior slopes of these lobes. In sum, each of these specimens shows different combinations of the "sapidus"-"sapidus acutidens" complex.

The paratype male "acutidens" from Rio de Janeiro (USNM 19083) is not as acute spined as Panamanian material and the outer orbitals are rather blunt by "acutidens" standards.

In rather scanty material available from southern Brazil and Uruguay, though the "acutidens" form predominates, teeth are not so sharp as in Panama and the ridging of granules on the carapace is suppressed to give a smoothed effect reminiscent of that in North American specimens.

The first gonopods of males, one of the most reliable characters for separating species of *Callinectes*, offer no help in separating "typical" and "acutidens" forms of *sapidus*. This pair of appendages shows individual variation on a basic structural theme (Figure 21) having more correlation with age than with general body facies or geographic region. It is apparent that movable retrogressive spinules in the main row of spinules increase in length with age, and that there is no set arrangement except a tendency to an irregular grouping of slender subterminal spinules more erect than the proximal ones. The flared membranous tip has an irregular quadrilateral or elliptical shape.

Abdominal segments of mature females vary in shape, some (such as USNM 126789, Dominica) having the distal edge of the sixth segment broadened at its distal corners to an almost rectilinear form, whereas in most this segment tapers toward the telson.

Gonopores of the females vary in width of aperture and ornamentation of margins. The variations shown in Figure 23b, c represent some extremes, but there is no association of pattern with geography, the only constant being the elongate opening characteristic of species in which gonopods of males are long.

Distribution.—Occasionally Nova Scotia, Maine, and northern Massachusetts to northern Argentina, including Bermuda and the Antilles; Øresund, Denmark; the Netherlands and adjacent North Sea; southwest France (found twice); Golfo di Genova; northern Adriatic; Aegean, western

Black, and eastern Mediterranean Sea (Figure 26).

The extreme southern record by Ringuelet (1963) is substantiated by the figure in his paper. Records north of Cape Cod occur only during favorable warm periods (Scattergood, 1960).

Holthuis and Gottlieb (1955, 1958), Holthuis (1961, 1969), and Christiansen (1969) summarized the introduction of *C. sapidus* into Europe, and Bulgurkov (1968) extended the known range, recording an adult female taken in the western part of Varna Bay in October 1967. From these accounts it is clear that introduction in the Mediterranean and adjacent waters is an active one involving a breeding population, whereas the others seem to be temporary occurrences, but all are judged to have come from transport of small specimens in the ballast tanks of ships (op. cit., and Wolff, 1954a, 1954b). Banoub (1963) published one of the most complete accounts, noting that presence in Egypt does not seem to have been recorded before 1940. When *C. sapidus* was first noticed in Lake Manzilah, Egypt, it was confused with *Portunus pelagicus* (Linnaeus), itself an immigrant to the area from the Indian Ocean via the Suez Canal, and this confusion has persisted in literature on both species. Banoub thought that *C. sapidus* may have migrated from Greece around the eastern Mediterranean to flourish in the brackish lakes of Egypt, reproducing the life pattern it exhibits in the Western Hemisphere.

Habitat.—The blue crab is a coastal creature occurring on a variety of bottoms in fresh, estuarine, and shallow ocean from the water's edge to approximately 90 m (Franks et al., 1972), but mainly in the shallows to depths of 35 m. Biology of the species is better known than that of any other in the genus. Hatching in mouths of estuaries and shallow ocean, development of larvae progresses in the ocean (development studied both in nature and the laboratory), followed by migration of megalopae and young crabs back into estuaries to mature into adults (summarized in Williams, 1965, 1971; Tagatz, 1968; Taissoun, 1969; and literature compilation, Tagatz and Hall, 1971). It is probable that all species in the genus carry out their life histories on this model.

Tolerant of extremes, the species has been found from fresh water to hypersaline lagoons such as Laguna Madre de Tamaulipas, Mexico, where collections have been made in salinities ranging from 44 to 48‰ and unproductive portions of the lagoon range up to 117‰ (Hildebrand, 1957), in temperatures ranging from 3° to 35°C, and in tertiary sewage treatment ponds in which mean daily O_2 tension dropped as low as 0.08 mg/liter in summer (Smith, 1971). In Lebanon it has been collected in winter in 39‰ salinity water at 17.5°C where there is no good place for estuarine development because streams are small, seasonal, and exceedingly foul in dry weather (George and Athanassiou, 1965). In Marion Co., Fla., large males have been taken from salt springs in the St. Johns River over 180 miles from the sea.

Often considered a scavenger, which it certainly is, the normal diet includes a variety of materials including fishes, benthic invertebrates, and plant material (Darnell, 1959; Tagatz, 1968). Odum and Heald (1972) confirmed this assessment, finding mainly an abundance of small mussels in stomach contents of individuals in a marsh in SW Florida.

Spawning.—Most spawning occurs in spring and early summer, warm months helping to assure survival of larvae. Females with egg masses have been found in North Carolina from mid-March to late November. Northward the season is somewhat shorter and to the south (United States) it is longer (Williams, 1965). Early spring spawners may cast a second batch of eggs in late summer contributing to a lengthened spawning season or a secondary late summer peak. The number of eggs per spawning has been estimated at 700,000 to more than 2 million (Williams, 1965). Ovigerous females in museum collections are rare, but suggest that at least some eggs are spawned almost the year round in tropical waters. Taissoun (1969) showed this to be true in the Golfo de Venezuela where ovigerous females are most abundant between April and September, reaching a sample maximum of 75% in July and August. Also, in the northern part of Bahía del Tablazo, Venezuela, ovigerous females occur during all of the year except between August and November, reaching a sample maximum of 95% in May. Absence of ovigerous females there in late summer and fall occurs because heavy rainfall and increasing river flow freshen the area, driving females downstream to areas of higher salinity; consequent increases of ovigerous females occur in the Golfo de Venezuela during August and September.

Economic importance.—Though all species of *Callinectes* are consumed as human food, there is

no doubt that *C. sapidus* is the most valuable in commercial fisheries, providing a highly acceptable, nutritious product worth several million dollars annually in the United States alone. Traditionally, the seat of this fishery in the United States has been Chesapeake Bay where records on the fishery have been kept for about a century. Pearson (1948), summarizing annual catch for this area from 1880 to 1942, showed the annual catch to have increased from 9.5 million pounds in 1890 to a peak of 68.7 million pounds in 1930. Catch, however, fluctuated before and after 1930, declining to 35.8 million by 1942 during World War II. Van Engel (1962) provided a history of the types of gear used in this fishery, an evolution from hand-dip trotline to the baited crab pot (trap) and dredge. Adoption of the baited pot and its spread to the Carolinas and elsewhere during the late 1950's, along with other methods of capture including incidental harvest of crabs from shrimp trawls, greatly expanded the catch. By 1967 (latest available annual summary) the U.S. fishery landed nearly 150 million pounds of hard and soft crabs worth 10 million dollars (Lyles, 1969).

The species is harvested throughout its range either as an object of commercial enterprise or for home use. Taissoun (1969, and pers. commun.) reported a growing industry in Venezuela. Banoub (1963) reported growth of an Egyptian fishery in lakes (poor flavor) and sea (good flavor), but remarked on losses from damage to nets and on the myriads of crabs having no local commercial value because the Egyptians consider the meat unpalatable (Fishing News International, 1965). A developing fishery in Northern Greece (Kinzelbach, 1965) declined because of overfishing (Boschma, 1972).

Fossil record.—I have reviewed the fossil material treated by Rathbun (1919a, b, 1935) and more recent acquisitions in collections of the USNM and U.S. Geological Survey (USGS) and concluded that only two specimens can be positively identified as *C. sapidus*. Eighteen lots of specimens are probably *Callinectes*, and some of these are possibly *C. sapidus*, but most of the remains are too fragmentary for positive identification. The entire record ranges from lower Miocene of Florida to Pleistocene of Maryland and New Jersey, material identifiable to species probably being limited exclusively to the Pleistocene.

Published records of Pleistocene occurrence include *Lupa dicantha* (= *C. sapidus*) from sandy beds in Wadmalaw Sound, S.C. (Holmes, 1858), a two-thirds grown specimen of *C. hastatus* (= *sapidus*) in a concretion from excavation for a Hudson River Tunnel on the New Jersey side (Whitfield, 1891), a male *C. sapidus* from near the mouth of Choptank River at Cook Point, Dorchester Co., Md., and fragmentary remains from Wailes Bluff near Cornfield Harbor, and Federalsburg, Md., as well as Heislerville, N.J. (Clark, 1906), all cited by Rathbun (1935).

USGS 25272. (= Locality of Tulane University Department of Geology, Field No. 546). Eight-foot (+) vertical exposure 0.52 mi (0.84 km) due E Florida hwy. 84 (30°29′55″N, 85°11′32″W) along N bank of prominent sharp bend in Ten Mile Creek, Calhoun Co., Fla. Material collected "in situ" from the lower 3 ft (0.9 m) of section. Chipola Formation; late Lower Miocene. Paul E. Drez, summer, 1972, on loan from Warren C. Blow, Paleontology and Stratigraphy Branch, USGS. (A) A well-preserved right palm and one-third of propodal finger, facets bearing resemblance to *C. declivis* on external face, but hand broad and flat dorsally as in females of modern *Callinectes*, molar complex absent. (B) One disarticulated right dactyl with broken tip having moderate-sized, worn, proximal tooth. (C) One rather large, straight, right propodal finger with sectorial teeth.

USGS 25273. Fifteen foot (4.6m) vertical exposure along S bank Mattiponi River, just below White Oak Lodge at White Oak Landing (about 2.5 mi [4 km] E King William Courthouse) King William Co., Va. Material collected "in situ" between 1 and 2.5 ft (30-76 cm) above beach level in a blue gray, highly burrowed, sparsely fossiliferous, silty sand (devoid of mollusks) which overlies a highly fossiliferous shell bed consisting of abundant *Turritella*. "Virginia" St. Marys Formation; Middle Miocene. Lauck W. Ward, 1961, on loan from Warren C. Blow, Paleontology and Stratigraphy Branch, USGS. An immature female *Callinectes* with triangular abdomen (length about 23 mm from posterior edge of exposed segment 3 to tip of telson) and broad sternites, few remnants of carapace not coarsely granulate.

USGS 25274. White Oak Landing, about 2.5 mi (4 km) E King William Courthouse, along S bank Mattiponi River, King William Co., Va. Material collected as "float" along 400 ft (120 m) (+) beach between tributary just below landing proper and

next tributary upstream. The material, though "float," apparently washed out of the lower bed of the "Virginia" St. Marys Formation, which outcrops along this beach. Lauck W. Ward, 1961, on loan from Warren C. Blow, Paleontology and Stratigraphy Branch, USGS. Three immature specimens of *Callinectes*. Two females with broad sternites and triangular abdomen exposed; (A) a half-grown individual with fragmented abdomen distorted (abdomen length about 29 mm from posterior edge of exposed segment 3 to estimated tip of telson); (B) a much smaller individual with incomplete abdomen (abdomen length about 12 mm from posterior edge of exposed segment 3 to estimated tip of telson; (C) cephalothorax of an immature individual about 45 mm wide, with broad sternal plates as well as areolations of carapace suggesting *C. sapidus*, frontal and anterolateral teeth missing, abdomen unexposed, shape of telson suggesting a female.

USGS 25275. "Road fill" NW side of Virginia hwy. 360, along both sides of Manquin Creek, King William Co., Va. Material is "spoil" thought to be derived from nearby road cut(s) during construction of addition to hwy. 360. Age unknown, probably Yorktown Formation; Late Miocene. Lauck W. Ward, 1961, on loan from Warren C. Blow, Paleontology and Stratigraphy Branch, USGS. Large, complete right palm (dorsal length about 30 mm), propodal finger, and mold of dactyl broken out of a concretion; palm heavily ridged, facets between ridges reticulated as in *C. reticulatus* (internal mold of hand), but remnants of exoskeleton externally smooth except for granules on ridges; portion of finger remaining resembling *Callinectes* with proximal enlarged tooth on dactyl and molar apparatus on propodal finger. The palm is compressed in preservation, but appears as broad in restoration as a modern *Callinectes*.

USGS 3859. Pleistocene (Miocene?), "tonged up in the Rappahannock River near the Chesapeake Bay by an oysterman" and sent to the Smithsonian Institution in 1902 by W. McD. Lee. Flattened partially crushed central portion of an adult male *C. sapidus*, including part of carapace with regions exposed and sternum with abdomen missing. The dark color of the specimen only suggests similarity to other Pleistocene (Miocene?) material from the area of origin, for exact horizon is unknown.

USNM 371729, Pleistocene, Broadwater, Va., R. Phillips. A large adult male fragment consisting of a deformed carapace (length 67, width at base of lateral spines 127 mm) along with a right cheliped lacking fingers. The chela is disarticulated. Shape of abdomen, carapace, and carpus of cheliped with no internal spine indicate *C. sapidus*.

Seven lots from the Pleistocene, Wailes Bluff, St. Marys Co., Md., treated in part by Rathbun (1935) and Blake (1953), are similar to Modern *C. sapidus* but lack definitive characters.

USNM 145356. Talbot Formation, Bd. 1 (of Mansfield), 1937, S. F. Blake. Immature male with carapace and sternum exposed.

USNM 146701. Frank Burns, 1886, Stn. No. 2032. Portion of left minor dactyl and right propodal finger.

USNM 371726. Talbot Formation, L. W. Stephenson, W. C. Mansfield, and W. P. Popenoe, 26 June 1925, (10902). Portion of left propodal finger and hand, and nearly intact right propodal finger.

USNM 371727. Talbot Formation, W. C. Mansfield, 8-12 June 1920 (8932). Fragments of a left chela (propodus), tips of two fingers, and fragments of a minor chela.

Uncatalogued lot. (Bd. 1), R. J. Taylor, 15 June 1941. Mostly fragments of four right propodal fingers, six left propodal fingers, and one complete right dactyl.

Uncatalogued lot. (Bd. 1), R. J. Taylor, 15 June 1941. Three immature female and one immature male fragmentary sterna.

Uncatalogued lot. Pamlico Formation, W. E. Salter. Two dactyls from right and left chelae.

Five lots from Pleistocene, Cape May and Atlantic Counties, N.J., similar to modern *C. sapidus*.

USNM 371930. Cape May Formation, Stone Harbor, H. G. Richards. A short section of finger.

USNM 371933, Cape May Formation, Two Mile Beach, H. G. Richards. A short, stocky propodal finger with well developed molar complex.

USNM 371934. Cape May Formation, Two Mile Beach, H. G. Richards. Five central portions of right propodal fingers of half- to full-grown individuals, three central portions of left propodal fingers of comparable size, two proximal portions of probable left dactyls of large crabs, and three other pieces possibly broken from above.

USNM 371936. Cape May Formation, Two Mile Beach, H. G. Richards. Tooth row and tooth sockets on finger, probably a dactyl.

Uncatalogued lot. Brigantine I., Atlantic Co., H. B. Roberts, May 1953. A large, somewhat crushed right chela with proximal half of fingers.

Remarks.—Resolution of the taxonomic confusion surrounding the correct name for *C. sapidus* by Holthuis (1962) greatly simplifies both discussion of the species' systematic history and variability over its range. From Latreille's (1825) description, it is apparent that the original material from Philadelphia (possibly not the actual site of collection) indeed represented the "typical" form from eastern North America. Holthuis' selection of a lectotype from this material and Williams' (1965) restriction of the type locality to "east coast of the United States" support the facts as well as they can be known today. Search of the collection at ANSP revealed no specimens of *C. sapidus* that date from the time of Latreille, and it is almost certain that specimens on which he based his description are lost. There is no need now to designate a new type specimen, indeed selection of a neotype would not be in keeping with the spirit of the International Code (Art. 75), for no complex zoological problem now depends upon a specimen for its solution in this case.

The earliest "scientific" treatment of the species (Bosc, 1802) was more a natural history account than a description, the name *Portunus hastatus* being taken from a description paraphrased from J. C. Fabricius (1798) that applied to the European species originally described as *Cancer hastatus* by Linnaeus (1767).

I consider the whole *C. sapidus* complex to be a single species which has diverged into ill defined populations in certain portions of its range. The "acutidens" form predominates over most of the latitudinal range, but there are variations. Among these are "typical" features that reach their most pronounced expression in the population along the east coast of the United States. Taxonomic thinking of biologists has been clouded by the fact that the form originally described was the North American variant which became the standard against which all comparisons were made.

Callinectes sapidus is the member of the genus which has most successfully invaded the Temperate Zone, and in this respect it may be that speciation into forms associated with temperature regimes is progressing, but the process is not yet complete enough that morphological separation is distinct.

Material.—Total: 460 lots, 1,500+ specimens. Specimens listed in Rathbun (1930) from USNM (45656 and 26092 not found), MCZ, and BMNH.

USNM. 284 lots, 1,060+ specimens, including the following not cited above plus 7 lots and 13 specimens from undetermined localities and 2 lots of fingers from Indian mounds.

UNITED STATES

Massachusetts: 122952, Deadneck, Cotuit, Barnstable Co., 1 July 1949, 1 ♂, 3 ♀ (juv), H. E. Winn.

New York: 63260, Sing Sing [Ossing], no date, 1 ♂, 1 ♀, A. K. Fisher.

New Jersey: 63177, 63178, 63181, off New England Creek, 19 Oct. 1929, 2 ♂, 1 ♀ (juv), H. G. Richards. 63179, 1 mi off Dennis Creek, 13 Aug. 1929, 3 juv, H. G. Richards. 77006, 77041, Dennis Cove, 13 and 25 Aug. 1929, 61 juv, H. G. Richards. 77007, 77040, Barnegat Bay, Lavalette, 15 Aug. 1931, 2 ♂, 3 ♀, 4 juv, H. G. Richards.

Delaware: 77037, Delaware Bay near Woodland Beach, no date, 1 ♂ (juv), Coltam and Saylor. 63180, Mispillion River, 10 July 1929, 1 ♂ (juv), H. G. Richards. 77039, Mispillion Cove, 26 Aug. 1931, 3 ♂ (juv), H. G. Richards.

Maryland: 92452, Wye River, 16 Aug. 1951, 1 ♂, M. Sandoz. 113230, Sullivan Cove, Severn River, 31 Aug. 1966, 1 ♂, deformed chela, B. Truett. 77036, Lake Ovington, near Bay Ridge, 19 July 1936, 3 ♂, 2 ♀ (juv), C. R. Aschemeir. 76996, mouth Patuxent River, Solomons I., 16 July 1934, 2 ♀ (juv), P. Bartsch. 77033, Coster, about 3 mi N Solomons I., no date, 1 ♂, deformed chela, B. Coster. 67646, Coster, no date, 1 ♀, albino, W. Everett. 76148, Point Lookout, 9 Sept. 1932, 1 ♀ (juv), E. Bowles. 77004, Ridge, St. Marys Co., 26 Apr. 1930, 1 ♂ (juv), W. H. Ball. 76129, Blakistone I., 9 Sept. 1932, 1 ♀ (juv), E. Bowles. 66326, Herring Creek (Lower Potomac), 31 July 1929, 5 ♀ (juv), B. A. Bean. 66328, 77000, Riverside, 21 Nov. 1912, 2 ♂, 3 juv, U.S. Bur. Fish. 66614, Cobb I., Rock Point, Potomac River opposite Colonial Beach, 14 Aug. 1931, 1 ♂, E. D. Reid, W. L. Brown, and W. Pike. 75448, Analostan I., Potomac River at Georgetown, D.C., 11 Sept. 1930, 2 ♂, W. Reynold. 81473, 81474, Crisfield, 7 Oct. 1941, 41 juv, W. L. Schmitt. 95733, off Smiths I., 20 Aug. 1953, 1 ♂, partial albino, J. M. Ingley.

Virginia: 61146, Tangier, Dec. 1927, 1 deformed chela, J. Parks. 76998, Smiths I., 5 July 1935, 4 juv, W. H. Ball. 77034, Smiths I., Northampton

Co., 6 July 1935, 1 ♂, Lombino. 63320, Cape Charles, no date, 1 ♂, 1 ♀ (juv), H. G. Richards. 112857, Chesapeake Bay (believed to be in southwest middle grounds area), 15 Oct. 1964, 1 ♂, H. A. Martin. 67739, Elizabeth River, Portsmouth, 16 June 1933, 1 ♂, deformed chela, W. L. Hughes. 81483, Craney Island Lab., Norfolk, no date, 1 ♀ (juv), F. F. Ferguson. 81485, U.S. Public Health Serv., Craney I., Norfolk, Aug. 1940, 1 ♀, F. F. Ferguson. 76184, Virginia Beach, 4 July 1932, 2 carapaces (dry), G. E. Brandt.

North Carolina: 107137, Currituck Sound, 15 Nov. 1960, 1 ♂ (juv), J. A. Kerwin. 122964, Currituck Sound, no date, 1 ♂ (juv), J. R. Davis. 60601, Hatteras, May 1927, 67 ♂, 23 ♀, A. J. Poole and R. Kellogg. 107477, approx. ½ mi S Silver Lake Inlet and Ocracoke Village, 6 Aug. 1958, 2 ♀, col. unknown. 62462, Gallant Point, Beaufort Harbor, 13 Sept. 1928, 3 ♀ (juv), Schmitt and Shoemaker. 76999, Beaufort, no date, 1 ♂, col. unknown. 77002, Newport R. above "narrows," Beaufort, 3 Apr. 1931, 1 ♂ (juv), S. F. Hildebrand. 77003, Beaufort, 29 Sept. 1929, 1 ♂ (juv), Hobbs and Maloney.

South Carolina: 17191, South or North Carolina, no date, 1 ♀, *Fish Hawk* Stn. 6850.

Florida: 99892, Sewall Point, Martin Co., 27 Feb. 1955, 1 ♂ (juv), D. K. Caldwell, et al. 122944, Deep Lake, Miami, 5 Apr. 1952, 2 ♂, H. Field and Y. Lazor. 122949, Little Duck Key on S side of Rt. 1, Dade Co., 21 Dec. 1962, 1 juv, E. Kotkas and R. Chandler. 122950, Beach area and tidal flats on S ridge of Bahia Honda Key, Monroe Co., 3 Aug. 1965, 1 juv, N. R. Foster and D. G. Smith. 71606, S side of County Road, Key West, 13 Nov. 1922, 1 juv, Stephenson. 77038, Marquesas Keys, 11 Aug. 1931, 7 juv, A. S. Pearse. 77031, between Long and Bush Key, Tortugas, 26 July 1931, 1 ♀, A. S. Pearse. 77030, Tortugas, 25 June 1931, 1 ♂, W. L. Schmitt. 122958, Charlotte Harbor, 13 Sept. 1939, 1 ♀ (juv), USFWS Launch 58, hauls 1, 2, 3. 122953, Sarasota near Cape Haze Marine Lab., 26 Jan. 1966, 1 ♀, 4 juv, R. F. Cressey and R. H. Brown. 122954, Sarasota, near Cape Haze Marine Lab., 27 Jan. 1966, 2 juv, R. F. Cressey and R. Brown. 71654, Sarasota Bay, summer 1930, 4 juv, W. W. Wallis. 122943, Homasassa Springs, 30 Mar. 1946, 1 ♂, Herald and Strickland. 122929, Hernando Co., Gulf of Mexico, Gulf Beach and March outlet to Gulf at Pine I., 8 mi NW Weekiwachee Springs, 7 Apr. 1955, 2 ♂, 3 ♀ (juv), R. D. Suttkus and Sylvia A. Earle. 77566, Cedar Key, 25 Jan. 1938, 1 ♂, 15 juv, C. R. Aschmeier. 98085, Choctawatchee Bay, no date, 1 deformed chela, col. unknown. 122951, Florosa, Okaloosa Co., 3 Dec. 1941, 4 ♂ (juv), W. F. Blair. 66753, Florida, no date, 1 ♂, 1 ♀, Ross Allen.

Alabama: 81480, Big Lake, Gulf State Park, 14 Oct. 1939, 1 ♂, col. unknown.

Mississippi: 85543, Mississippi Sound, east end, 1 Sept. 1947, 1 ♂, J. W. Ward, et al. 122947, inside Petit Bois I., Mississippi Sound, 20 Apr. 1967, 1 ♂, 2 ♀, *George M. Bowers* Stn. 4, 5.5 m. 122938, Simmons Bayou trib. to Davis Bay, 2 mi SE Ocean Springs, 2 Aug. 1957, 1 ♂ (juv), R. D. Suttkus. 90299, S side of Cat I., Mississippi Sound, 9 Aug. 1949, 1 ♀ (juv), col. unknown. 2028, Washington [Adams Co.], no date, 1 ♂, Wailes. 77035, coast, May 1937, 1 ♀, J. S. Dolley.

Louisiana: 69676, Ycloskey [Bernard Parish], 10 June 1934, 2 ♀, J. N. Gowanloch. The following from Point aux Herbes, Lake Pontchartrain, 122940, 15 July 1955, 4 ♂, 18 ♀ (juv), R. R. Lubritz. 122939, 22 June 1955, 83 juv, R. R. Lubritz. 122927, 4 June 1955, 80+ juv, R. D. Suttkus. 122926, 4 June 1955, 1 ♂, 1 ♀ (soft), R. D. Suttkus. 122928, W Pearl River immediately above, N of Mill Bayou, St. Tammany Parish, 11 Aug. 1955, 1 ♀, M V *Lyman* Stn. 136. 122934, 1¼ mi up West Pearl River from mouth, St. Tammany Parish, 11 Aug. 1955, 1 ♀, M V *Lyman* Stn. 138. 122933, Lake Pontchartrain, Salt Bayou, 9 June 1955, 10 juv, R. D. Suttkus. 122935, 2.5 mi NW Salt Bayou on Pearl River, St. Tammany Parish, 11 Aug. 1955, 1 ♀, M V *Lyman* Stn. 143. 122936, ¼ mi SE West Pearl River Bridge, Lake Pontchartrain, St. Tammany Parish, 11 Aug. 1955, 1 ♂, M V *Lyman* Stn. 144. 122930, Lake Pontchartrain, first point W Liberty Bayou, 9 June 1955, 2 juv, M V *Lyman* Stn. 18. 122931, St. Joe Channel [Lake Pontchartrain], 21 June 1954, 2 parasitized, Patursan and Peterson. 97992, Lake Pontchartrain just S mouth of Tanipahoa River, 17 Oct. 1953, 11 ♂, 2 ♀, R. M. Carnell. 96990, Lake Pontchartrain, no date, 1 ♀ parasitized, col. unknown. 96322, Rigolets, Lake Pontchartrain, 29 Oct. 1953, 1 ♀ deformed carapace, L. Eddy. 122932, Rigolets at Lake Borgne, 7 June 1955, 1 ♀ (juv), R. D. Suttkus. 122960, Lake Pontchartrain at mouth of Tchefuncta River, St. Tammany Parish, 1 Apr. 1948, 2 ♀, R. M. and M. K. Bailey. 122945, Lake Pontchartrain, Aug. 1962, 1 ♂, J. Q. Burch. 64145, off Breton I., Nov. 1930, 1 ♂, S. Springer. 122963, 3-6 mi ESE of SW Pass, 16 Feb. 1934, 1 ♂, T. C. D., M. J. L., and W. W. A. 122959, [S of Plaquemines Parish] 29°01′N, 89°33′W, 8 July 1938, 1 ♀, *Pelican* Stn. 77-2. 105317, Barataria Bay, Jefferson

Parish, 27 Feb. 1960, 1 ♂, 4 ♀ (parasitized), E. H. Behre. 122937, Grand Isle, 3 Feb. 1957, 1 ♂, 1 ♀, R. D. Suttkus. 122961, [off Caillou Bay] 28°39.5′N, 91°04.5′W, 11 July 1938, 1 ♀, *Pelican* Stn. 81-2. 122962, on 9-fathom line between Ship to Trinity Shoal Buoy, 28°39.5′N, 91°04.5′W, 11 July 1938, 3 ♀, *Pelican* Stn. 81-2. 122956, 28°51.5′N, 91°33′W to 28°56.5′N, 91°50′W, 11 July 1938, 2 ♂, 2 ♀, *Pelican* Stn. 82-1 to 82-5. 5509, Louisiana, 1883, 2 ♂, 1 ♀, R. W. Shufeldt.

Texas: 78397, Galveston Bay, Galveston Co., 16 Apr. 1939, 3 ♀, C. E. Burt. 122957, Galveston, 4 May 1941, 1 ♂, 3 ♀ (2 juv), J. L. Baughman. 122955, Galveston south of ferry landing, 27 Aug. 1965, 1 ♀ (juv), J. McCain. 122948, south end, west side new Galveston-Houston causeway, Galveston, 24 Aug. 1965, 1 juv, J. C. McCain. 122946, 17 mi S, 7 mi E Alvin, Brazoria Co., 28 July 1952, 1 ♂, S. Alvin. 122942, Freeport, 12 May 1940, 1 ♀ (ov), J. L. Baughman. 122941, Alligator Head, Matagorda Bay, no date, 13 juv of ♀ form parasitized (dry), J. D. Mitchell. 81479, Aransas Pass, 8 July 1941, 1 ♂, 2 ♀ (soft and 2 parasitized), J. L. Baughman. 99243, Laguna Madre, 15 mi N of Port Isabel, 24 Jan. 1956, 2 juv, col. unknown. 71663, Texas, no date, 1 ♂, C. T. Reed. 81475, Texas, no date, 1 ♂ (juv), col. unknown.

JAMAICA

120626, Fresh River headwaters, N end of Caymanas Plantation, St. Catherine Parish, 7 Apr. 1959, 1 ♂, Hart, G. Thomas, R. Bengry, Thornton.

PUERTO RICO

80667, no date, 1 ♀ (recently ov, bearing jar label "nov. var?"), S. T. Danforth. 77044, Río Canovanillas, Canovanas [18°23′N, 65°55′W], 16 Feb. 1934, 2 ♂, S. F. Hildebrand.

VIRGIN ISLANDS

The following from St. Croix: 71524, Fairplain, no date, 1 ♂, 1 ♀ (juv), H. A. Beatty. 71794, Fairplain Stream, Dec. 1934, 1 ♀ (juv), H. A. Beatty. 72337, Fairplain Stream, 1935-36, 1 juv (soft), H. A. Beatty. 72356, Fairplain stream below bridge, 1935-36, 2 ♂, H. A. Beatty. 77032, on sea coast, Rust-op-Twist, no date, 1 ♀, H. A. Beatty.

GUATEMALA

123096, Atlantic at Punta Marrabique, N of Puerto Barrios, 1 May 1947, 1 ♂, R. R. Miller. 123097, Lago de Izabal, 26 Apr. 1947, 1 ♂, Miller et al.

COSTA RICA

113278, Tortuguero, May 1964, 1 ♂, 1 ♀, D. P. Kelso.

PANAMA

77043, Gatun Locks, C.Z., 21 Feb. 1935, 12 juv, S. F. Hildebrand.

VENEZUELA

The following from Golfo de Venezuela: 123099, 11°46′N, 71°16′W, 6 Oct. 1965, 1 ♀, *Oregon* Stn. 5670. 123095, 11°33′N, 71°31′W, 6 Oct. 1965, 1 ♀ *Oregon* Stn. 5672. 123100, 11°27′N, 71°39′W, 6 Oct. 1965, 4 ♀, *Oregon* Stn. 5673. 80649, Lago de Los Pájaros, 1 km above Lago de Maracaibo, 30 Apr. 1942, 2 ♂, L. P. Schultz. 80650, Lago de Maracaibo, 20 Feb. 1942, 2 ♀ (juv), L. P. Schultz. 80651, Lago de Maracaibo, 7-9 Apr. 1942, 2 ♂, L. P. Schultz. 80652, Cāno de Sagua, 25 km N Sinamaica, 12 Mar. 1942, 3 ♀, L. P. Schultz.

BRAZIL

Rio de Janeiro: 77042, Recreio dos Bandeirantes, 9-16 Feb. 1935, 1 chela, D. M. Cochran. Santa Catarina: 123098, Nov. 1965, 1 ♀ (juv), Jones-Lowe.

URUGUAY

99848, Roca Arroya de Balizas [= Valizes?], Jan.-Feb. 1953, 2 ♀, R. Vaz-Ferreira.

AHF. 6 lots, 10 specimens.

UNITED STATES

Florida: Pompano Beach, Sept. 1943, 1 ♀, E. R. T. Marco I., Collier Co., 10 Mar. 1946, 1 ♀ (juv), *Velero* A87-46. Santa Rosa Sound at Camp Navarre, 12 May 1949, 2 ♂, Stn. LM4-49.

Louisiana: Lake Borgne, 27 Aug. 1954, 1 ♀, R. Darnell.

MEXICO

Veracruz: Drainage ditch 5 mi W Veracruz, 19 Aug. 1949, 1 ♀ (juv), B. W. Halstead. Boca del Río, 9 Aug. 1949, 1 ♂, 3 ♀, B. W. Halstead.

AMNH. 19 lots, 26 specimens, including 4 lots with no data.

UNITED STATES

Massachusetts: 1002, Chappaquiddick I., Martha's Vineyard, 28 July 1909, 1 ♂ (dry), R. W. Miner.

New York: 221, New York Harbor, no date, 1 ♂, 1 ♀, L. P. Gratacap. 6267, Mastic, Long Island, Aug. 1930, 1 ♂, J. T. Nichols. 9856, Hudson River opposite Spuyten Duyvil, Sept. 1945, 1 deformed chela, J. Dvorak. 9778, Sheepshead Bay, N.Y. City, 1944, 1 ♂, H. Savalli. 6316, Freeport, Long Island, 5 Oct. 1930, 1 ♀, F. Limekiller. 6258, Inner Harbor, Cold Spring, Long Island, 26 July 1930, 1 ♂, C. H. Curran. 983, Fort Schuyler, N.Y. City, no date, 1 ♂, and extra chelae, E. Forshan.

New Jersey: 6491, Newark Bay, foot 27 St., Bayonne, 28 Aug. 1931, 1 ♂ (deformed chela), K. Wangler. 6653, Barnegat Bay, no date, deformed right chela (dry), col. unknown.

Florida: Lake Worth, July-Aug. 1945, 1 ♀, W. G. Van Name and A. H. Verrill. 10249, Destin, 29 July 1948, 6 juv, L. A. Burry.

BAHAMAS

Nassau and Andros I., Mar.-Apr. 1930, 1 ♀, Bacon-Miner Exped. and International Exped. to Andros.

CUBA

1024, 1913, 1 juv, J. T. Nichols.

PUERTO RICO

2787, Tallaboa [18°00'N, 66°43'W], 29 July 1914, 1 ♂ (juv), R. W. Miner.

ANSP. 26 lots, 41 specimens.

UNITED STATES

North America: 35, [Delaware Bay], no date, 1 ♀ (dry) Blanding.

New Jersey: 2798, along coast, no date, 2 ♀ (dry), W. M. Wood. 2933, Ventnor, Aug. 1928, 1 deformed chela (dry), R. D. Benson, Jr. 3659, Great Egg Harbor, no date, 1 ♂ (dry), S. Ashmead. 3604, Point Breeze, Delaware River, no date, carapace, F. L. LeCompte. Delaware River, 30 July 1951, 2 ♂, 1 ♀, J. Bates.

Maryland: Potomac River at Popes Creek, Charles Co., Aug. 1966, 3 ♂, 1 ♀ (juv), S. L. H. Fuller. Potomac River ¼ mi above Lower Cedar Pt., WNW Morgantown, Charles Co., Aug. 1966, 3 ♀ (juv), S. L. H. Fuller. 3492, Chesapeake Bay, no date, 1 ♂ (dry), from U.S. Explor. Exped.

Virginia: York River, 31 May 1956, 1 ♀, F. A. Aldrich. York River, 2 June 1956, 3 ♀ (1 ov), F. A. Aldrich. York River, 21 Sept. 1956, 1 ♂, 1 ♀, F. A. Aldrich. James River, 17 June 1957, 1 ♂, F. A. Aldrich.

North Carolina: 4873, Fort Macon, 2 ♀, Yarrow.

Florida: 3481, Key West, no date, 1 ♀ (juv), S. Ashmead. 3569, Manatee River, no date, 1 ♂ (dry), S. Ashmead.

Texas: Houston-Galveston Ship Canal, July 1954, 1 ♂, 1 ♀ (juv), F. A. Aldrich. Cow Bayou, trib. of Sabine River, Orange Co., 11 Aug. 1962, 1 ♂, C. W. Hart, Jr. Sabine River, Orange Co., 9 Aug. 1962, 2 ♂, C. W. Hart, Jr. Sabine River, N of Sabine I., Orange Co., 13 Aug. 1962, 2 ♂, C. W. Hart, Jr.

CUBA

4697, Cojímar near La Habana, 10 July 1940, 2 ♀, R. A. McLean.

DOMINICAN REPUBLIC

3519, no date, 1 ♂ (dry), W. M. Gabb. 2957, no date, 1 ♀ (dry), W. M. Gabb.

PUERTO RICO

3179, off Guánica Harbor, no date, 1 ♂ (dry), Fowler.

PANAMA

1305, no date, 1 ♀ (juv), McNeil Exped.

BRAZIL

3514, no date, 3 ♂ (dry), T. B. Wilson.

BMNH. 15 lots, 28 specimens.

UNITED STATES

Connecticut: 98.5.7.312, Long Island Sound, 1 ♂, 1 ♀, Norman. 80.26, New Haven, 1 ♀, Norman.

New Jersey: 98.5.7.317/18, 3 ♂, 1 ♀ (juv) Verrill and Smith. Unreg., Cape May, 1 ♂ (dry) vi/9, J. K. Townsend. Unreg., 1 ♀ (juv, dry) vi/6.

Maryland: 1964.9.7.13, Chesapeake Biological Lab. Pier, Solomons, 1 ♂ (juv), F. J. Schwartz and A. C. Edwards. 1964.9.7.14/16, Patuxent River at Evans pier, Solomons, 1 ♂, 1 ♀ (juv), A. C. Edwards and F. J. Schwartz.

Florida: 1966.12.5.555/557, coast of Everglades Park, 3 juv, U. Miami, Inst. Mar. Sci. 1966.12.5.667, 1 ♂, Univ. Miami, Inst. Mar. Sci. 1966.12.5.666, 1 ♂, Univ. Miami, Inst. Mar. Sci. 1966.12.5.668/671, 4 juv, Univ. Miami, Inst. Mar. Sci.

TOBAGO

1925.1.28.11/12, 1 ♂, 1 ♀, P. L. Guppy.

TRINIDAD

1940.7.8.15, 1 ♂, A. K. Totton.

BRAZIL

Unreg. 1 ♀ (juv, dry) vi/6, col. unknown.

MCZ. 42 lots, 159 specimens.

BERMUDA

5122, no date, 1 ♀ (juv), Bickmore.

UNITED STATES

Massachusetts: 322, Cohasset, 1922, 1 ♀, J. A. Murphy. 5110, Naushon I., Buzzards Bay, 1873, 2 ♀, W. Faxon. 333, Pocasset, 1919, 1 ♀, J. A. Cushman.

Connecticut: 5563, New London, no date, 2 ♂, 3 ♀, G. G. Hammond, Aug. 1876. 8510, New London, no date, 3 ♂, 10 ♀, G. G. Hammond, 1876.

New York: 332, Fishers I., 1874, 1 ♀ (ov), Hyatt and Rathbun. 5471, 1 ♂, 2 ♀, L. Agassiz, 1859.

New Jersey: 5112, Somers Point [N shore across from Ocean City], no date, 3 ♂, 3 ♀, W. Stimpson, recd. Oct. 1864. 5212, Somers Point, no date, 50 juv, W. Stimpson, recd. Dec. 1864.

Maryland: 5117, Baltimore, 1860, 2 ♂, A. Hyatt.

North Carolina: 11351, 2 mi SE Roanoke I., 19 Dec. 1940, 1 ♂, R. Foster. 11353, 5 mi SW Nags Head, near Roanoke I., Dec. 1940, 1 ♂ (juv), R. Foster. 5113, Beaufort, no date, 3 ♂, 3 ♀ (juv), A. S. Bickmore.

South Carolina: 5116, Waccamaw, no date, 1 ♀, L. Agassiz. The following from Charleston: 5114, no date, 2 ♂, 2 ♀, L. Agassiz (part of Ordway's material). 5202, no date, 2 ♂, 12 ♀, col. unknown. 8751, no date, 1 ♂, 1 ♀, T. Lyman.

Georgia: 5201, May 1859, 1 ♂, T. S. Allanson.

Florida: 5205, June 1859, 1 ♀, G. Wurdemann. 8752, no date, 6 ♂, col. unknown. 11936, Key West, May 1940, 2 juv, J. R. Miller. 5118, Tortugas, 2 ♂, Jacques, from Peabody Acad. Sci. Nov. 1885. 5203, Fort Jefferson, Tortugas Is., no date, 2 ♂, col. unknown. 10163, Sanibel I., Mar. 1938, 3 ♂, 3 ♀, F. A. Chace, Jr. 5119, Charlotte Harbor, 1 ♂, L. Gibbes, recd. 13 Feb. 1861. 8334, Lemon Bay and Gulf, Englewood, Sarasota Co., Jan.-Apr. 1935, 2 ♂, 2 ♀, 3 juv, D. J. Zinn.

Alabama: 5204, Mobile, no date, 1 ♂, 1 ♀, 2 juv, L. Agassiz.

Mississippi: 11942, Ship I. off Biloxi, June 1941, 1 juv, J. R. Miller.

Louisiana: 12046, Bayou La Fourche near Shriever, June 1941, 1 ♂, J. R. Miller.

Texas: 5120, no date, 1 ♂, G. Wurdemann. 5121, Galveston, 1871, 1 ♀, Boll.

CUBA

5123, La Habana, no date, 1 ♂, S. Garman. 10887, Cienfuegos [22°09'N, 80°27'W], 19 Feb. 1938, 1 ♀, Harvard-Havana Exped.

HAITI

5213, Jérémie. Apr. 1865, 1 ♂, 1 ♀, D. F. Weinland.

MEXICO

Yucatán: 8623, Progreso, 1904, 1 ♂, L. J. Cole.

BRAZIL

The following from Rio de Janeiro: 5126, no date, 1 ♂, Thayer Exped., recd. 1865. 5127, no date, 1 ♂, Thayer Exped. Estado de Rio Grande do Sul: 4699, Rio Grande, June 1861, 1 ♂, Harrington.

MNB. 1 lot, 1 specimen.

BRAZIL

Santa Catarina: 57, Ponta do Farol, São Francisco do Sul, 1 ♀, recd. July 1901.

MNHNP. 1 lot, 1 specimen, plus 3 specimens in old dry collection.

FRANCE

Rochefort, 1900, 1 ♂, from M. Vieuille.

RMNH. 49 lots, 109+ specimens.

UNITED STATES

East coast of N America, Sept. 1836, 1 ♂, 1 ♀, G. Troost.

Connecticut: 401, New Haven, no date, from Smithsonian Inst.

New York: 13790, Shinnecock Bay, Long Island, Oct. 1955, 4 juv, A. Perlmutter.

New Jersey: 15253, Creek at Stone Harbor, Cape May Co., 8 May 1960, 2 ♀, juv, J. L. Scheltema.

Delaware: 11407, 11408, Delaware Bay, juv, date and col. unknown. 11344, Delaware Bay about 1 mi off Lewes, Sussex Co., 27 Apr. 1957, 1 ♀, L. B. Holthuis.

Maryland: 14616, Mouth of Potomac River, Point Lookout, St. Marys Co., 20 Mar. 1960, 2 ♀, J. L. Scheltema. 9827-9832, Chesapeake Bay, series of juv from 6 localities, date and col. unknown. 9833, mouth of harbor at Snowhill Landing, Snowhill, Worcester Co., 30 Sept. 1952, 1 ♂, juv, L. B. Holthuis. 9836, northern portion of Chincoteague

Bay, N of Snowhill, Worcester Co., 29 Sept. 1952, 1 ♂, 1 ♀, L. B. Holthuis. 9837, Johns Creek at mouth of St. Leonards Creek in cove of Patuxent River, W of Lusby, Calvert Co., 16 May 1953, 1 ♀, L. B. Holthuis.

Virginia: 9838, Harborton, Accomack Co., 28 Sept. 1952, 1 ♀, L. B. Holthuis.

Florida: The following from Biscayne Bay—21351, off Rickenbacker Causeway, 1 Feb. 1965, 1 ♀, J. A. Cabrera and L. B. Holthuis. 23432, near Mathesan Hammock S of Miami, 3 Jan. 1965, 1 ♂, juv, L. B. Holthuis. 21346, S of Rickenbacker Causeway, Miami, 4 Feb. 1965, 1 ♀ (ov), L. B. Holthuis. The following from Bear Cut near Marine Lab., Virginia Key—24258, 1 Sept. 1965, 1 juv, J. A. Cabrera and L. B. Holthuis. 24259, 22 Dec. 1964, 1 juv, L. B. Holthuis. 18710, 2-9 Sept. 1963, 1 ♀, L. B. Holthuis. 15635, Marco Beach S of Marco, washed ashore by hurricane Donna, 12 Sept. 1960, 1 ♀, L. B. Holthuis. 15634, mangroves near Marco Beach S of Marco, 12 Sept. 1960, 1 ♀ (juv), L. B. Holthuis.

PUERTO RICO

23465, Rio Guánica, 15 Sept. 1963, 1 ♂, 1 ♀, P. W. Hummelinck.

TRINIDAD

23404, mouth of Diego Martin River [5 mi NNW Port of Spain], 1965-66, 2 ♂, H. O. von Hagen. 17738, Matura, NE coast of island, 19 June 1961, 1 ♂, I. Kristensen.

CURAÇAO

11881, Waaigat, Willemstad, 30 Jan. 1957, 2 ♀, L. B. Holthuis.

NETHERLANDS

23434, Friesland, washed ashore, 7 May 1967, 2 ♂, 1 ♀, T. P. Broerse. 24754, southern North Sea 25 mi NW Ijmuiden [14 mi WNW Amsterdam], 19 Jan. 1968, 1 ♀, Rijks. Inst. Visserij Onderzoek. Beach at Dishoek between Flissingen and Zoutelande, Zeeland, 20 Jan. 1967, a large right swimming leg (dry), G. R. Heerebout. Washed ashore at Vlissingen in cooked condition, Aug. 1950, carapace of adult ♀ (dry), A. C. Visser.

GREECE

Delta area of Axiós and Gallikós near Pírgos, Thessaloníki, 15 June 1964, part of ♀ carapace and abdomen, from shallow water in *Salicornia* fields, from fisherman, W. J. Wolff and M. Loosjes. 18689, fishmarket in Thessaloníki, from Gulf of Thessaloníki, 14 Mar. 1963, 1 ♀, R. Kinzelbach. Beach at Strimonikós Kólpos (= Gulf of Orfani) near Aspróvalta, about 15 km W Tsgezi (= Iraklítsa), 10 Mar. 1963, 2 rather worn carapaces (dry), R. Kinzelbach. 13082, Aegean Sea near harbor of Pórto Lágo, 29 June 1959, 2 ♀, C. Swennen.

TURKEY

21148, on S coast near Silifke (Seleucia), 19 Aug. 1964, 1 ♀, Turkey Excursion, 1964 from Hamburg Mus. 13137, E coast of Akyatan Lagoon 45 km S Adana, 18 May 1959, 4 ♂, 2 ♀.

ISRAEL

The following from Naaman River S of Acre: 18829, mouth of River, 2 Feb. 1955, 1 ♂ (juv), A. Perlmutter. 13795, near Acre, 13 Oct. 1955, 2 juv, A. Perlmutter. 13794, same, 17 Aug. 1955, 1 ♀, E. Gottlieb. 17840, between railroad bridge and mouth, 30 Apr. 1962, 2 ♂, 3 ♀, L. B. Holthuis. Mouth of river, 30 April 1962, carapace and chelae of 2 or more individuals (dry), L. B. Holthuis. 18832, Lagoon on Kishon River, N of Haifa, 31 Jan. 1955, 1 ♀, Sea Fish Res. Stn., Haifa. 10722, Mouth of Tiphlis River near Tantura, about halfway between Cesarea and Atlit, 26 Oct. 1955, 1 ♂ encrusted with *Chelonibia patula* (Ranzani), A. Perlmutter. 13793, Mouth of Hefzibah [Hadera?] River near Hadera, 21 Nov. 1951, 1 ♀ (juv), E. Gottlieb. 13792, Hefzibah, 21 Nov. 1951, 1 ♀ (juv), E. Gottlieb. 13791, Alexander River near mouth [S Hadera], 20 Dec. 1955, 1 ♀ (juv), E. Gottlieb.

SADZ-B. 7 lots, 27 specimens.

BRAZIL

Rio de Janeiro: 3240, Atafona, 12 July 1963, 10 ♂, 8 ♀, N. Meneses. 1721, Atafona, 1964, 1 ♂, N. Meneses. 950, S. João da Barra, Nov. 1911, 1 ♀, E. Garbe.

São Paulo: 1814, Santos, 11 Sept. 1962, 1 ♀, G. Melo. 1727, Guarujá, Jan. 1920, 1 ♀, Hempel.

Santa Catarina: 664, Itajaí, Dec. 1914, Luederwaldt.

Rio Grande do Sul: 3234, Praia de Torres, 5 Oct. 1964, 1 ♂, 2 ♀ (1 ov), J. Bertoletti.

UNC-IMS. 8 lots, 34+ specimens.

UNITED STATES

Delaware: 1853, Near Port Mahon, 1 July 1954, 2 ♀, H. J. Porter.

North Carolina: 2246, West Bay near Cedar I., Pamlico Sound, Carteret Co., 21 July 1969, 2 ♀ (ov), includes smallest mature ♀ on record, from fisherman. 821, Neuse River near New Bern, Craven Co., 24 July 1957, 1 ♂ (juv), Tagatz and Dudley. 738, Neuse River at Smith Farm, near North Harlowe, Craven Co., 1 Oct. 1957, 3 ♂, 1 ♀, juv, Judy and Dudley. 739, Neuse River at North Harlowe, 26 July 1957, 3 ♀ (juv), Tagatz and Dudley. 820, Pivers Island near Beaufort, Carteret Co., 27 May 1957, 1 ♂, 4 ♀ (juv), Talbot and Fischler. 913, off Beaufort Inlet, 26 Nov. 1959, 4 ♀ (3 ov), covered with *Chelonibia,* H. J. Porter.

PUERTO RICO

2136, Fresh water canal, 5 km S Lajas, 10 Feb. 1967, 3 ♂, 1 ♀ juv.

YPM. 1 lot, 1 specimen.

BRAZIL

6399, Rio Grande, 7 June 1860, 1 ♂ bearing *Chelonibia,* G. Harrington.

Supplementary literature records.—Nova Scotia (Piers, 1923); Maine and Nova Scotia (Scattergood, 1960); Bermuda (Verrill, 1908a, b); Laguna Madre de Tamaulipas, Mexico (Hildebrand, 1957); Alvarado, Veracruz, Mexico (Contreras, 1930); Dominica (Chace and Hobbs, 1969); Lago de Maracaibo and Golfo de Venezuela (Taissoun, 1969); Quenquén, Buenos Aires, Argentina [?] (Boschi, 1964); Elbe estuary, Germany (Kühl, 1965); Netherlands and North Sea localities (Holthuis, 1969); mouth of Gironde, France (Amanieu and Dantec, 1961); Gulf of Spezia and Genoa Harbor, Italy (Tortonese, 1965); northern Adriatic lagoons, Italy (Holthuis, 1961 [review]); Greece and parts of eastern Mediterranean (Serbetis, 1959); Beirut, Lebanon (George and Athanassiou, 1965); Buḥayrat Idkū and Buḥayrat Manzilah, Egypt (Banoub, 1963).

QUESTIONABLE SPECIES

Rathbun (1907) described *Callinectes alexandri* from Papeete, Tahiti, and Suva, Fiji Islands, on basis of two juveniles, and later (1911) noted a small mature male from Cragados, Carajos [Shoals, Mascarene Islands, Indian Ocean]. Stephenson and Campbell (1959) synonymized this confusing form with *Portunus pelagicus* (Linn.), commenting on its close similarity to members of *Callinectes* and temporarily questioning the validity of *Callinectes.* Later Stephenson et al. (1968) accepted the generic status quo. Stephenson (1968) confirmed his recognition of *Callinectes* and, after examination of Rathbun's specimens of *C. alexandri,* reidentified the Tahiti and Fiji material as *P. sanguinolentus* (Herbst) and the Indian Ocean specimen as *P. pelagicus.* The history of these bleached specimens emphasizes the difficulty in identifying some juvenile portunid material.

Chen (1933) described *Callinectes platei* on basis of a small male (length 14, width 29 mm), and *C. alcocki* on basis of a small ovigerous female (length 10.5, width including lateral spines 16 mm) from Tuticorin [Madras, India]. There is no sure way to identify these forms because specimens from the Plate collection are apparently no longer in existence. From the descriptions and figures, the two species possibly represent male and female of the same form, a small portunid with internal carpal spine. This alone is enough to remove them from *Callinectes.* Moreover, no known *Callinectes* is ovigerous at the tiny size of this female.

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ELECTROPHORETIC COMPARISON OF FIVE SPECIES OF PANDALID SHRIMP FROM THE NORTHEASTERN PACIFIC OCEAN

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ABSTRACT

Pandalid shrimp from off Alaska, Washington, and Oregon were investigated using starch-gel electrophoresis. Each species was found to be polymorphic for phosphoglucomutase, and the general protein patterns separated them into two groups—one consisting only of *Pandalus hypsinotus* and the other containing *P. borealis*, *P. goniurus*, *P. jordani*, and *Pandalopsis dispar*.

A key based on biochemical characters was developed which could separate the five pandalid species investigated.

The increase of commercial fishing for shrimp along the Pacific coast of North America in recent years has stimulated interest in the biology and identification of species and population units. Ronholt (1963) reported on the distribution and relative abundance of five species of pandalid shrimp from the northeastern Pacific Ocean. Butler (1965) presented a comprehensive report on the growth, reproduction, and distribution of pandalid shrimp in British Columbia waters, demonstrating the importance of inlets and bays to this group of crustaceans. Several reports on sampling techniques, diel vertical migration, and population movements have occurred which emphasize the need for additional information on the biology of pandalid shrimp for optimal utilization of this resource (Barr and McBride, 1967; Barr, 1970, 1971; Gotshall, 1972).

One of the more promising techniques for the detection of population units is the biochemical genetic approach, utilizing starch-gel electrophoretic separation of proteins coupled with histochemical staining procedures (Hunter and Markert, 1957). This method has been widely used and successfully applied to fisheries problems (reviewed by de Ligny, 1969, 1972).

This paper reports our application of starch-gel electrophoresis to separation of species and populations of five species of shrimp which occur along the coast of the northeastern Pacific ocean.

MATERIALS AND METHODS

Five species of adult pandalid shrimp from two genera were investigated; *Pandalopsis dispar*, *Pandalus borealis*, *P. goniurus*, *P. hypsinotus*, and *P. jordani*. All samples except those of *P. jordani* and one collection of *P. hypsinotus* were obtained from Marmot and Kazakof Bays of Kodiak Island, Alaska, during May 1972, and identified by personnel of the National Marine Fisheries Service at Kodiak, Alaska. These samples were shipped frozen to our laboratory where they were kept at −15°C until tested. Two collections of *P. jordani* were obtained off Coos Bay and Astoria, Oreg., in 1971 and identified by personnel of the Fish Commission of Oregon, shipped to us frozen and kept at −15°C until tested. Additional samples of *P. jordani* and *P. hypsinotus* were obtained during December 1972 from Bellingham Bay, Wash.

Extracts of muscle tissue were prepared by mixing equal volumes of tissue and 2% phenoxyethanol in distilled water into uniform pastes with glass rods. The starch-gel electrophoretic procedure followed the methods reported by Johnson, Utter, and Hodgins (1972). The buffer system used was described by Ridgway, Sherburne, and Lewis (1970). After electrophoresis the gels were sliced into four horizontal slices and stained for phosphoglucomutase (PGM), lactate dehydrogenase (LDH), tetrazolium oxidase (TO), peptidase (Johnson et al., 1972), malate dehydrogenase NAD and NADP (MDH), glyceraldehyde-3-phosphate dehydrogenase (GAPDH; Shaw

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and Prasad, 1970), naphthyl acetate and propionate esterases (modified after Utter, Stormont, and Hodgins, 1970), and general protein (Johnson et al., 1972).

RESULTS AND DISCUSSION

Bands of identical electrophoretic mobility for a given enzyme system were observed in all species for the following systems: MDH (NADP), one anodal band; MDH (NAD), one anodal band; peptidase (valyl-leucine), three anodal bands; TO, one anodal band; and GAPDH, three anodal bands.

Esterase patterns varied among species; however, the patterns were weak and not completely repeatable. Gasser and Rowlands (1972) noted similar problems in interpreting esterase patterns from human serum and related the differences to nongenetic causes. We have, therefore, excluded them from further consideration in this study. Esterases have been found useful in studies of other invertebrates and may indeed be of use in studies of pandalid shrimp if reliable methods can be developed for stabilizing expression of patterns (Manwell and Baker, 1970; Barlow and Ridgway, 1971).

Lactate dehydrogenase was expressed as one anodal band—with a broad, faint-staining area anodal to it—in each species. The bands of *P. jordani*, *P. borealis*, and *P. goniurus* had an identical mobility slightly more anodal than the bands of *P. hypsinotus* and *Pandalopsis dispar*.

The general protein patterns observed are shown in Figure 1. *Pandalus hypsinotus* had bands C, E, F, and G; *P. jordani* and *P. borealis*, bands A, B, D, and G; and *P. goniurus* and *Pandalopsis dispar*, bands A, B, and G. The B band, although qualitatively invariable, varied considerably in intensity in all species expressing it. A greater degree of difference in the protein pattern was observed between *Pandalus hypsinotus* (processing three unique bands) and the other four species than was observed among these four species.

Phosphoglucomutase (PGM) was polymorphic in all five species. Two-banded phenotypes (Figure 2) were observed in some individuals of all species, presumably reflecting heterozygous individuals, and the pattern suggests that the active PGM enzyme in shrimp is a monomer (Shaw, 1964). This agrees with reports of PGM polymorphisms found in vertebrates (see Johnson, Utter, and Hodgins, 1971). A diagrammatical representation of the allelic forms found within the five species (Figure 3) shows the six allelic bands that were observed and designated (in decreasing anodal mobility) A, B, C, D, E, and F. The distribution of these alleles, as indicated in Figure 3, was *P. hypsinotus*, A, B, E, and F; *P. goniurus*, A and B; *P. borealis*, C, E, and F; *P. jordani*, B, C, and E; and *Pandalopsis dispar*, C, D, and E. The phenotypic distributions of PGM in the five species of shrimp along with gene frequencies, Hardy-Weinberg calculations and collections data are presented in Tables 1 and 2. With the exception of *Pandalus hypsinotus*, the phenotypic distributions of PGM of the collections of shrimp species did not deviate significantly

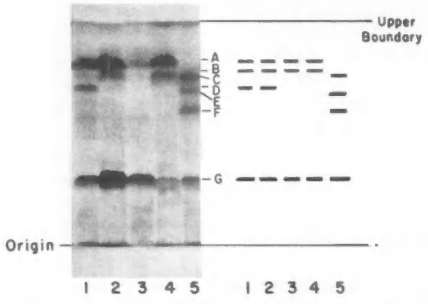

FIGURE 1.—Electrophoretic patterns on starch gel of muscle protein of five species of shrimp from the northeastern Pacific Ocean. Numbers below the patterns indicate the following species: 1. *Pandalus jordani*, 2. *P. borealis*, 3. *P. goniurus*, 4. *Pandalopsis dispar*, and 5. *Pandalus hypsinotus*.

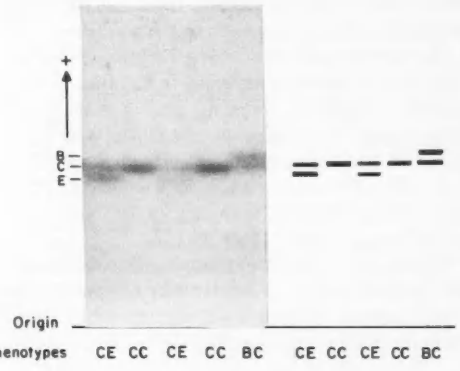

FIGURE 2.—Phosphoglucomutase phenotypes of *Pandalus jordani* in starch gels suggesting monomeric configuration of this enzyme.

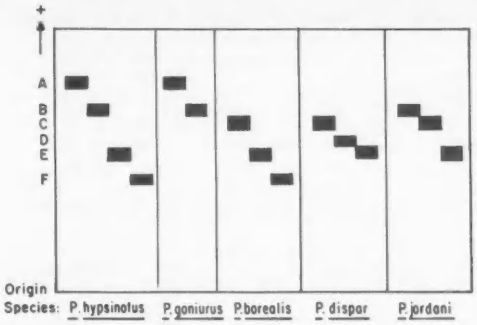

FIGURE 3.—Diagrammatical representation of the alleles of phosphoglucomutase in five species of pandalid shrimps as shown by the technique of starch-gel electrophoresis.

from expected Hardy-Weinberg values, and the gene frequencies of intraspecific samples were similar over the geographic range samples for *P. jordani*.

The collections of *P. hypsinotus* from Alaska showed highly significant deviation from Hardy-Weinberg expectations. Variation from expected Hardy-Weinberg proportions has also been observed for PGM variants of Pacific ocean perch, *Sebastes alutus* (Johnson et al., 1971) and related to depth of capture. Gene frequencies were similar for shallow- and deepwater collections; however, deepwater collections deviated significantly from expected Hardy-Weinberg frequencies. Further sampling stratified by depth (or other measurable variables) may reveal similar relationships for PGM variants of *P. hypsinotus*.

Inspection of the allele frequencies of the Alaskan and Washington collections of *P. hypsinotus* showed marked differences, especially with the A and E alleles (Table 1). These differences indicate that PGM variation may be useful in population identification of *P. hypsinotus*. Bullini and Coluzzi (1972) have presented evidence for selection of PGM alleles over a broad geographic range in mosquitoes *Aedes aegypti* and *A. mariae*. Additional sampling of *P. hypsinotus* may reveal a similar phenomenon as that found in the mosquito species.

The general protein, LDH, and PGM patterns observed in the five species were used to produce a key by which the species can be separated (Figure 4). This type of key should prove useful in application to shrimp identification problems.

CONCLUSION

The general protein patterns separated the species examined into two groups, one consisting only of *P. hypsinotus* and the other containing the remaining species of *Pandalus* and *Pandalopsis dispar*.

All five species of shrimp studied were polymorphic for PGM, with *Pandalus hypsinotus* possessing the greatest number of alleles (four

TABLE 1.—Phosphoglucomutase phenotypes of *Pandalus hypsinotus* taken off Alaska and Washington, 1971-72.[1]

Location	Sample size	Phenotypes of PGM									
		AA	AB	AE	AF	BB	BE	BF	EE	EF	FF
Alaska:											
Marmot Bay and Kazakof Bay	89	1 (1.8)	15 (9.0)	4 (8.5)	4 (4.1)	11 (11.5)	20 (21.5)	7 (10.3)	9 (10.2)	18 (9.8)	0 (2.3)
Washington:											
Bellingham Bay	80	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.9)	15 (14.6)	0 (0.1)	55 (55.5)	8 (8.9)	1 (0.0)

Location	Allelic frequencies				Test Data		
	A	B	E	F	df	χ^2	P
Alaska:							
Marmot Bay and Kazakof Bay	0.140	0.360	0.337	0.163	6	17.23	[2]$0.01>P>0.001$
Washington:							
Bellingham Bay	0.000	0.106	0.831	0.063	—	—	—
Contingency test comparing allelic composition of Alaska and Washington samples					3	89.64	$P<0.001$

[1]In parentheses are the expected values of a Hardy-Weinberg distribution.
[2]Chi-square test of Hardy-Weinberg distribution.

TABLE 2.—Phosphoglucomutase gene frequencies of four species of pandalid shrimp taken off Alaska, Oregon, and Washington; 1971-72.

Species and location	Sample size	Gene frequencies						Test data[1]		
		A	B	C	D	E	F	df	χ^2	P
Pandalus goniurus										
Alaska:										
Marmot Bay and Kazakof Bay	94	0.016	0.984	—[2]	—	—	—	1	2.34	0.2>P>0.1
Pandalus jordani										
Oregon:										
Coos Bay	150	—	0.010	0.980	—	0.010	—	3	0.00	P>0.99
Astoria	151	—	0.003	0.990	—	0.007	—	3	0.02	P>0.99
Washington:										
Bellingham Bay	79	—	0.000	1.000	—	0.000	—	3	0.00	P>0.99
Pandalus borealis										
Alaska:										
Marmot Bay and Kazakof Bay	418	—	—	0.059	—	0.934	0.007	3	7.60	0.1>P>0.05
Pandalopsis dispar										
Alaska:										
Marmot Bay	269	—	—	0.011	0.981	0.008	—	3	0.00	P>0.99

[1]Chi-square test of Hardy-Weinberg distribution.
[2]Indicates not observed in this species.

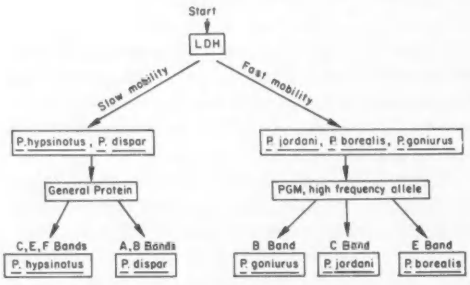

FIGURE 4.—Key to five species of pandalid shrimp based on three biochemical characters.

alleles). This polymorphism may prove useful for separation of breeding groups and as genetic markers in shrimp culturing experiments.

All five species could be identified based on a biochemical key that was developed.

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DISTRIBUTION AND RELATIVE ABUNDANCE OF LARVAE OF KING CRAB, *PARALITHODES CAMTSCHATICA*, IN THE SOUTHEASTERN BERING SEA, 1969-70

EVAN B. HAYNES[1]

ABSTRACT

During the spring and summer of 1969 and 1970, larvae of the king crab, *Paralithodes camtschatica*, were abundant in plankton samples from the southeastern Bering Sea. Abundance was highest near shore and generally lowest in the central and western parts of the study area. As the season progressed, the center of abundance moved northeastward along the Alaska Peninsula toward the head of Bristol Bay. This change in distribution was apparently related to water current patterns.

This report is based on collections of larvae of king crab, *Paralithodes camtschatica*, made by the Auke Bay Fisheries Laboratory, National Marine Fisheries Service, Auke Bay, Alaska, in the spring and summer of 1969 and 1970 in the southeastern Bering Sea. The larvae were collected during studies of migrating salmon and exploratory fishing for shellfish. In this report, I describe the distribution and relative abundance of the king crab larvae in the southeastern Bering Sea in 1969 and 1970 and relate seasonal changes in the distribution of the larvae to current patterns.

The only reports on distribution and abundance of king crab larvae in the study area are those by Takeuchi (1962, 1968) and Rodin.[2] Takeuchi sampled with various types of plankton nets from Japanese crab processing ships off the Black Hills-Port Moller area in 1957, 1958, and 1960. He found more king crab larvae off Port Moller than the Black Hills area, but because his sampling was restricted in area, he could not determine where the larvae had been released or where they dispersed. Rodin's study encompassed a greater area than Takeuchi's but was of shorter duration (less than 1 mo as compared with an average of nearly 2 mo). Rodin speculated, however, that king crab larvae were released primarily in the Port Moller area.

My study provided further evidence that a major area of release of king crab larvae occurs in the Black Hills-Port Moller area and the larvae generally disperse northeastward along the Alaska Peninsula toward the head of Bristol Bay.

MATERIALS AND METHODS

A total of 249 plankton tows were made in the southeastern Bering Sea from May to September 1969, and 237 were made from March to September 1970. Ten-minute oblique hauls were taken from the bottom to the surface during daylight with paired bongo nets (Posgay, Marak, and Hennemuth, 1968), each with a mouth area of 0.03 m^2 and nylon netting of 0.333-mm mesh. Tows were made at a speed of about 3 knots without regard to tide stage. The plankton samples were preserved in 5% Formalin[3] and seawater immediately after they were collected.

Although flowmeters were inside each sampler to determine the amount of water strained, mechanical difficulties prevented an accurate measure for most tows. However, the data have been converted to numbers of larvae under 10 m^2 of sea surface, as an index sufficiently precise to determine the general distribution and relative abundance of the larvae. Because the correlation between the two nets fished simultaneously was high ($r = 0.979$) and it is desirable to use whole numbers, I summed the catch of the two nets in

[1]Auke Bay Fisheries Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 155, Auke Bay, AK 99821.

[2]Rodin, V. E. 1966. Soviet investigation in 1965 to determine the status of king crab (*Paralithodes camtschatica* (Tilesius)) stocks in southeastern Bering Sea. Unpubl. manuscr., 12 p. Auke Bay Fisheries Laboratory, National Marine Fisheries Service, NOAA, Auke Bay, AK 99821.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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each tow rather than use the average in my analysis. The terms "positive tow" and "negative tow" are used to describe plankton tows that contained king crab larvae and those that did not. The station locations and developmental stages of king crab larvae captured for the positive tows are given in Table 1; the locations of both positive and negative tows are indicated in the charts showing distribution of larvae (Figures 1 to 7). Charts showing distribution and abundance of larvae were made by plotting the number of larvae under 10 m^2 of sea surface at each station and then drawing isopleths. Identification of the larval stages was based on descriptions given by Marukawa (1933), Sato and Tanaka (1949), and Kurata (1964).

TABLE 1.—Station location and number and stage of development of king crab larvae captured for each positive tow collected in the southeastern Bering Sea, 1969 and 1970.

Date	Depth (m)	Station location		Larval stage					
				Zoea				Glaucothoe	Total
		Lat. N	Long. W	I	II	III	IV		
1969									
May									
18	55	55°00′	165°00′	39	32	5	—	—	76
19	45	58°00′	163°22′	1	—	1	—	—	2
20	75	56°20′	162°12′	10	—	—	—	—	10
26	116	55°20′	165°45′	—	1	7	—	—	8
26	107	55°40′	165°10′	—	4	10	7	—	21
27	116	55°40′	165°47′	—	—	6	4	—	10
29	44	57°40′	163°22′	—	1	—	—	—	1
June									
3	45	56°20′	161°00′	5	18	8	4	—	35
3	63	57°00′	160°57′	4	13	6	—	—	23
3	63	57°00′	159°43′	49	60	1	—	—	110
3	47	57°40′	159°38′	5	1	1	—	—	7
4	57	57°40′	160°53′	8	1	—	—	—	9
4	47	58°00′	160°51′	4	2	—	—	—	6
4	40	58°00′	162°07′	1	—	—	—	—	1
5	75	56°20′	162°12′	—	2	2	—	—	4
17	19	56°03′	160°58′	—	—	—	2	—	2
18	63	57°00′	160°57′	—	—	—	2	—	2
19	63	57°00′	159°43′	2	23	20	6	—	51
19	47	57°40′	159°38′	2	9	—	—	—	11
19	57	57°40′	160°53′	2	3	1	—	—	6
19	47	58°00′	160°51′	—	3	5	—	—	8
20	46	57°40′	162°08′	1	2	—	—	—	3
20	60	57°00′	162°10′	—	—	1	1	—	2
24	66	56°40′	160°59′	—	1	—	4	—	5
24	68	56°30′	160°59′	—	—	2	1	—	3
24	45	56°20′	161°00′	—	—	1	6	—	7
26	68	56°30′	160°59′	—	—	3	7	—	10
27	29	56°54′	159°08′	—	—	—	1	—	1
27	36	57°00′	159°07′	—	—	—	1	—	1
27	45	57°09′	159°05′	—	—	2	3	—	5
27	51	57°20′	159°04′	—	2	9	5	—	16
28	51	57°29′	159°03′	—	5	42	7	—	54
28	44	57°40′	159°01′	—	—	11	—	—	11
28	35	57°49′	159°00′	—	1	8	1	—	10
28	37	57°55′	158°59′	—	—	5	1	—	6
29	43	58°00′	158°58′	—	—	4	1	—	5
July									
1	45	58°10′	160°50′	—	—	—	1	—	1
1	47	58°00′	160°51′	—	—	3	2	—	5
2	63	57°00′	160°57′	—	—	—	4	—	4
4	25	57°31′	158°54′	—	—	—	1	—	1
4	29	57°41′	158°17′	—	—	—	—	1	1
4	35	57°47′	158°23′	—	—	—	1	—	1
7	22	58°33′	159°31′	—	—	—	—	1	1
7	23	58°29′	159°32′	—	—	—	—	3	3
7	28	58°14′	159°30′	—	—	—	1	—	1
8	35	57°55′	158°33′	—	—	—	4	—	4
8	36	57°44′	158°20′	—	—	—	6	—	6
9	51	57°20′	159°04′	—	—	1	4	—	5
9	45	56°20′	161°00′	—	—	—	—	1	1
13	63	57°00′	159°43′	—	—	—	4	—	4
14	47	57°40′	159°38′	—	—	2	29	—	31
14	57	57°40′	160°53′	—	—	—	1	—	1
1970									
March									
29	111	55°08′	165°12′	1	—	—	—	—	1

TABLE 1.—Continued.

Date	Depth (m)	Station location		Larval stage					
				Zoea				Glaucothoe	Total
		Lat. N	Long. W	I	II	III	IV		
1970—Continued									
May									
9	60	55°00′	164°35′	399	20	2	—	—	421
13	73	56°40′	163°23′	1	—	—	—	—	1
13	75	56°20′	162°48′	1	3	—	—	—	4
14	47	55°40′	162°50′	16	9	—	—	—	25
14	76	56°00′	162°14′	26	2	—	—	—	28
14	75	56°20′	162°12′	2	—	—	—	—	2
15	65	56°40′	162°11′	1	—	—	—	—	1
15	65	57°00′	161°34′	1	—	—	—	—	1
16	65	57°20′	161°32′	2	—	—	—	—	2
16	55	57°20′	160°56′	1	—	—	—	—	1
16	58	57°20′	160°18′	11	2	—	—	—	13
16	63	57°00′	159°43′	1	—	—	—	—	1
17	35	56°40′	159°45′	9	1	—	—	—	10
17	58	56°40′	160°22′	9	—	—	—	—	9
17	58	57°00′	160°20′	12	1	—	—	—	13
17	63	57°00′	160°57′	7	—	—	—	—	7
18	66	56°40′	160°59′	14	2	—	—	—	16
18	86	56°40′	161°35′	20	1	—	—	—	21
18	61	56°20′	161°37′	40	10	2	—	—	52
19	45	56°20′	161°00′	163	106	—	—	—	269
19	25	56°20′	160°25′	5	3	—	—	—	8
22	73	56°10′	162°14′	11	4	—	—	—	15
22	52	56°06′	161°53′	4	1	—	—	—	5
22	70	56°26′	161°59′	16	7	—	—	—	23
23	71	56°40′	161°22′	3	1	—	—	—	4
23	60	56°26′	161°33′	35	17	—	—	—	52
24	22	57°07′	160°52′	1	—	—	—	—	1
24	47	56°19′	161°04′	9	2	—	—	—	11
24	70	56°31′	161°17′	36	22	—	—	—	58
24	83	56°43′	161°30′	3	1	—	—	—	4
24	64	56°55′	161°42′	6	2	—	—	—	8
24	51	57°07′	161°55′	4	—	—	—	—	4
25	36	58°02′	161°33′	1	—	—	—	—	1
25	22	58°13′	160°08′	1	—	—	—	—	1
26	45	57°41′	159°50′	2	1	—	—	—	3
26	45	57°29′	159°37′	3	1	—	—	—	4
26	51	57°17′	159°25′	2	1	—	—	—	3
26	47	57°06′	159°12′	5	12	—	—	—	17
26	21	56°54′	159°00′	—	2	—	—	—	2
28	89	55°52′	163°17′	1	—	—	—	—	1
28	59	55°39′	163°04′	1	—	—	—	—	1
29	111	55°33′	165°36′	—	1	1	—	—	2
29	111	55°21′	165°24′	—	12	4	—	—	16
29	111	55°08′	165°12′	—	2	1	—	—	3
29	91	54°56′	164°59′	—	13	1	—	—	14
29	43	54°43′	164°47′	2	5	2	—	—	9
June									
8	111	55°08′	165°12′	1	36	36	1	—	74
15	48	56°19′	161°00′	1	7	15	5	—	28
21	49	56°22′	161°00′	—	4	3	—	—	7
21	42	56°17′	161°00′	—	4	2	4	—	10
25	27	56°09′	161°00′	—	—	5	11	—	16
25	21	56°07′	160°52′	—	—	2	8	—	10
26	47	56°19′	161°04′	—	1	—	1	—	2
26	70	56°31′	161°17′	—	2	—	—	—	2
26	83	56°43′	161°30′	—	—	2	—	—	2
26	64	56°55′	161°42′	—	2	1	—	—	3
26	51	57°07′	161°55′	1	—	—	—	—	1
27	47	57°06′	159°12′	—	—	15	18	—	33
27	51	57°17′	159°25′	—	2	38	16	—	56
27	45	57°29′	159°37′	—	3	23	7	—	33
27	45	57°41′	159°50′	—	4	34	4	—	42
27	42	57°54′	159°42′	—	—	15	9	—	24
27	22	57°59′	157°55′	—	—	—	1	—	1
27	33	58°04′	158°25′	—	—	—	1	—	1
28	22	58°13′	160°08′	—	—	—	2	—	2
28	41	58°38′	162°16′	—	—	—	1	—	1
29	40	58°22′	163°24′	—	1	—	—	—	1
30	59	55°39′	163°04′	—	—	1	1	—	2
30	28	55°27′	162°52′	—	—	—	1	—	1
July									
1	111	55°33′	165°36′	—	—	—	—	1	1

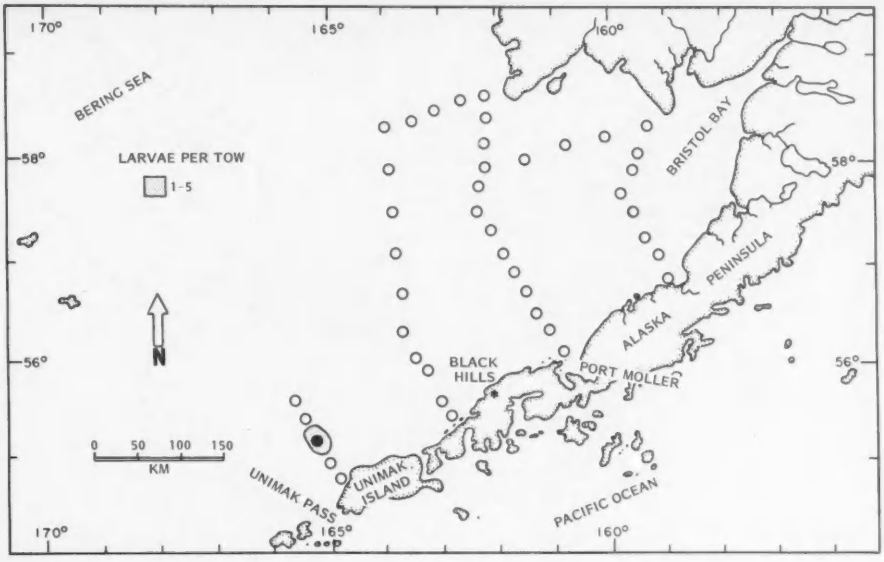

FIGURE 1.—Distribution and relative abundance of king crab larvae sampled at stations in the southeastern Bering Sea, 29 March-30 April 1969 and 1970. Solid circle indicates larvae were present at station.

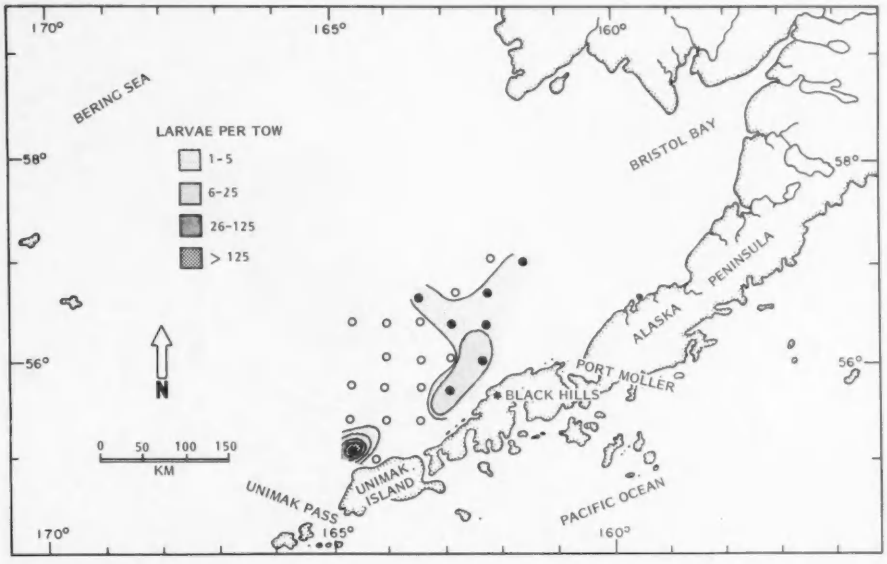

FIGURE 2.—Distribution and relative abundance of king crab larvae sampled at stations in the southeastern Bering Sea, 1-15 May 1969 and 1970. Solid circles indicate larvae were present at station.

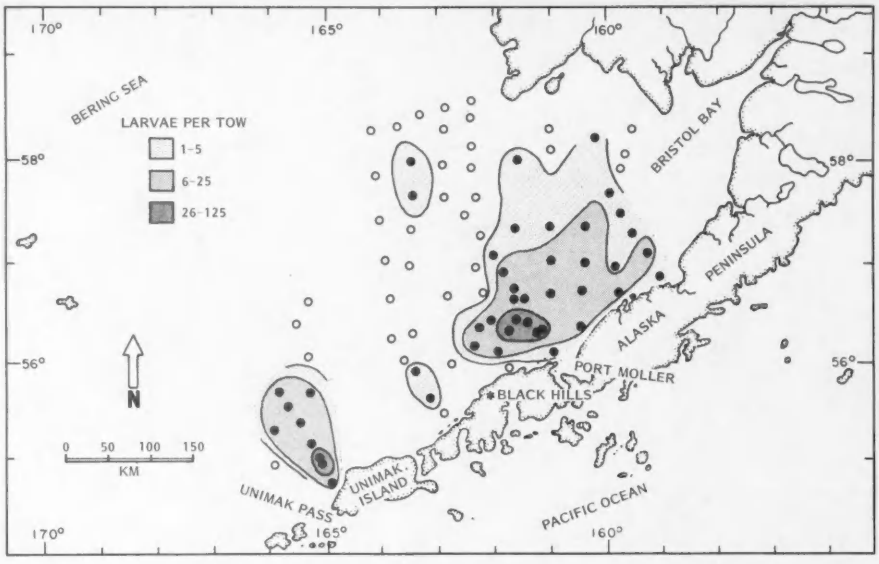

FIGURE 3.—Distribution and relative abundance of king crab larvae sampled at stations in the southeastern Bering Sea, 16-31 May 1969 and 1970. Solid circles indicate larvae were present at station.

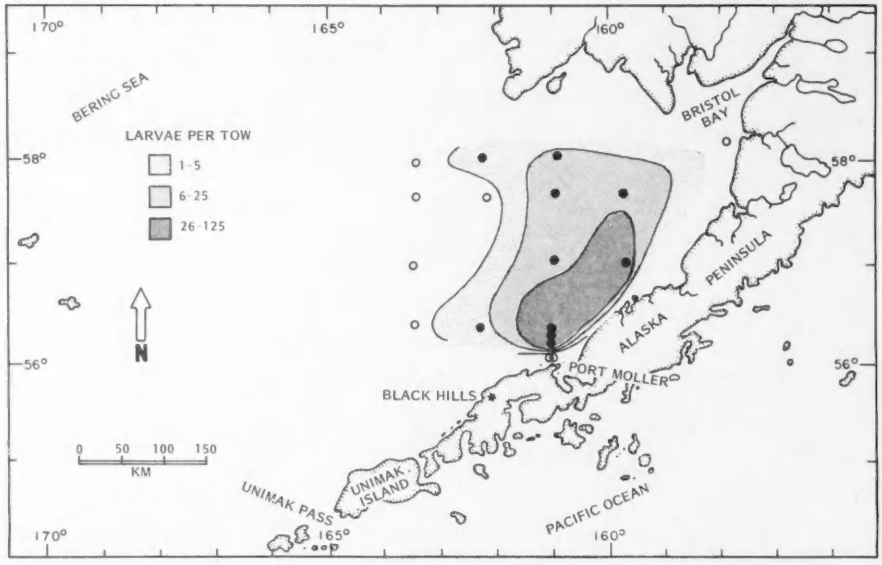

FIGURE 4.—Distribution and relative abundance of king crab larvae sampled at stations in the southeastern Bering Sea, 1-15 June 1969 and 1970. Solid circles indicate larvae were present at station.

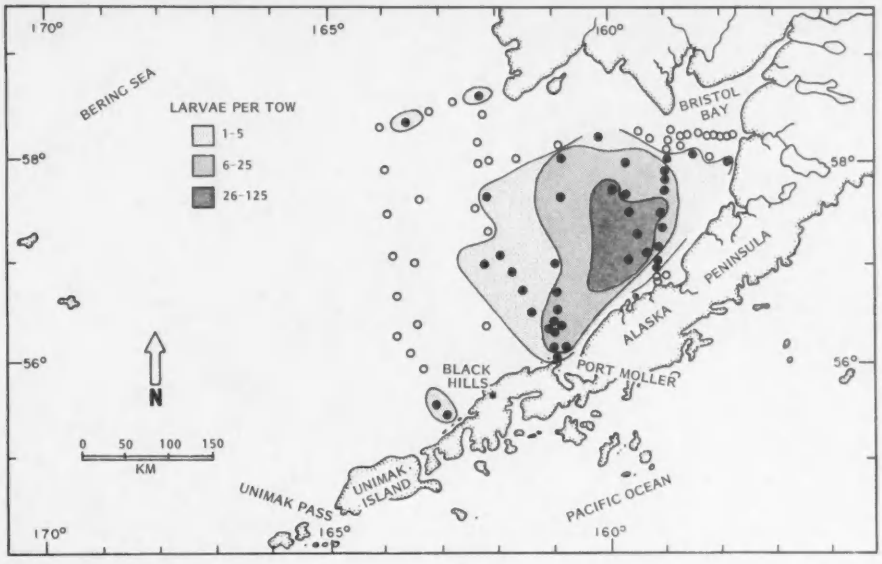

FIGURE 5.—Distribution and relative abundance of king crab larvae sampled at stations in the southeastern Bering Sea, 16-30 June 1969 and 1970. Solid circles indicate larvae were present at station.

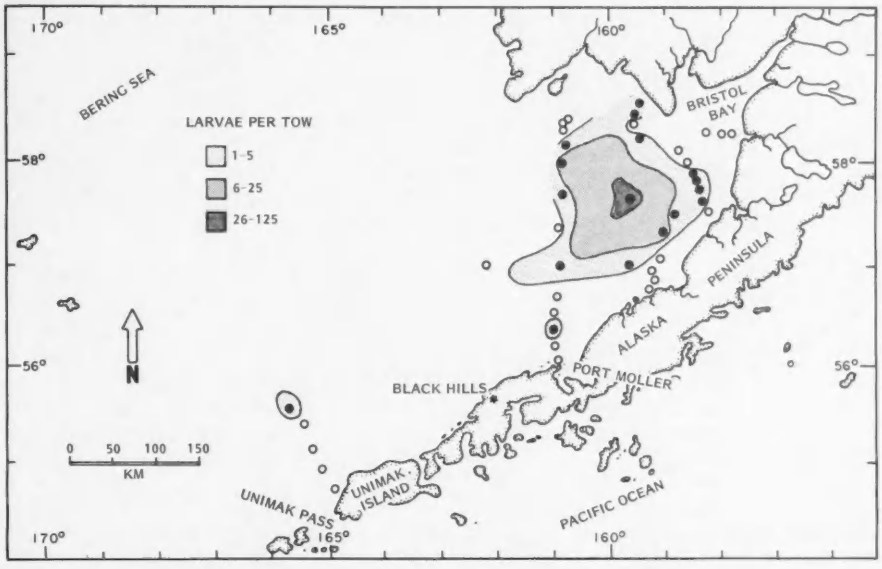

FIGURE 6.—Distribution and relative abundance of king crab larvae sampled at stations in the southeastern Bering Sea, 1-15 July 1969 and 1970. Solid circles indicate larvae were present at station.

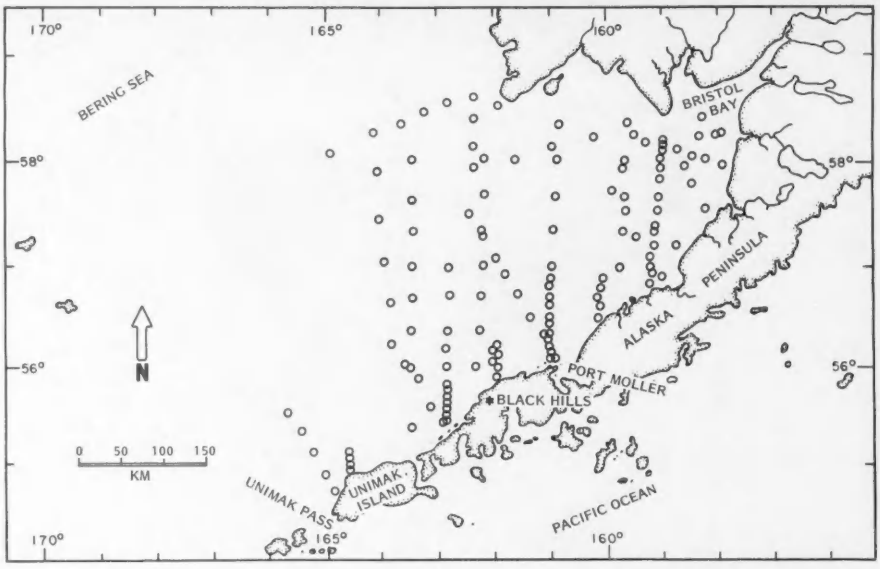

FIGURE 7.—Distribution and relative abundance of king crab larvae sampled at stations in the southeastern Bering Sea, 16 July-21 September 1969 and 1970.

DISTRIBUTION AND RELATIVE ABUNDANCE

Although sampling locations and dates were different each year, I determined that I could combine the data for both years for consideration of distribution and abundance. For each semimonthly period, I tabulated the degree squares (the areas bordered by 1° of latitude and longitude) that were sampled in both years. This resulted in 14 degree squares, 7 each for the latter half of May and June. For each of the two semimonthly periods, the median catch per tow was computed and the degree squares were ranked "good" or "poor" on the basis of whether their catch per tow was greater or lesser than the median. In this manner it was possible to compare degree squares without considering the actual abundance of larvae. The degree square data indicated that in every instance except one the same degree squares for each year were consistently good or poor.

I assumed therefore that the distributions were not random and that the data for the two sampling years could be combined for analyzing larval distribution.

The combined data on distribution of larvae in 1969 and 1970 are presented by time periods (usually semimonthly) between 29 March and 21 September (Figures 1 to 7). Most of the larvae were in the southern and eastern portions of the study area and within these areas were most abundant close to shore. The largest catches (more than 1,000 larvae under 10 m^2 of sea surface) were made near Unimak Pass and Port Moller; the smallest (usually fewer than 10 larvae under 10 m^2 of sea surface) were generally made in the more central and western parts of the area.

The distribution and abundance of larvae in the Black Hills-Port Moller area increased gradually toward the head of Bristol Bay. During the first half of May (Figure 2), larvae were found off the Black Hills area; 2 wk later (Figure 3), these larvae apparently had been carried northeastward along the coast and became mixed with larvae released off the Port Moller area. As the season continued, the center of abundance shifted farther toward the head of the bay (Figures 4 and 5). This trend continued until mid-July (Figure 6), when no more larvae were taken (Figure 7).

The seasonal progression of occurrence of larvae off Unimak Island is less clear. A small concentration of larvae was found in this area in early May (Figure 2); 2 wk later they were most abundant to

the northwest toward the open sea (Figure 3). Too few samples were taken in the Unimak Island area after May to determine the extent of the drift of larvae.

The four zoeal stages that king crab larvae pass through before molting to the glaucothoe (settling) stage were all represented in my samples (Table 1). The percentage of larvae in each zoeal stage is shown by semimonthly intervals in Figure 8. A comparison of this figure with Figures 1 to 7 shows that the progression of larval stages corresponded closely with the seasonal progression of larval distribution. For instance, the abundant larvae found early in the season off Unimak Island and Port Moller were mostly stage I. As the areas of greatest abundance moved toward the head of the bay, the percentage of later larval stages in the samples increased, and by July most of the larvae were stage IV (Figure 8).

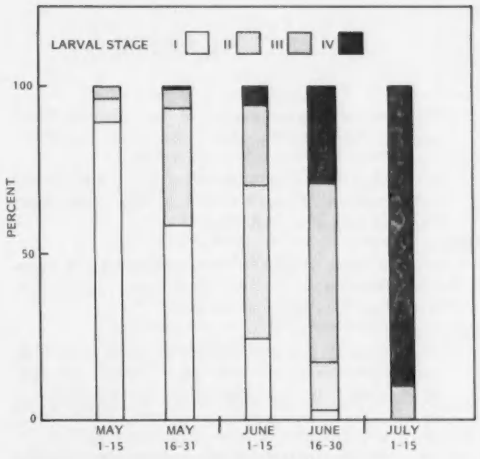

FIGURE 8.—Percentages of four zoeal stages of king crab larvae sampled at stations in the southeastern Bering Sea, 1969 and 1970. Data for 1969 and 1970 combined by semimonthly periods (see Figures 3 to 7).

LARVAL RELEASE AREAS

Areas of relatively high abundance of stage I larvae are generally assumed to be the areas where the larvae were released by the female. This proved to be true in the present study: stage I larvae were abundant near Unimak Island and the Black Hills-Port Moller area where female king crabs with empty egg cases were also abundant (Figure 9). (The egg cases remain attached to the pleopods of the female for some time after the larvae have been released.) The

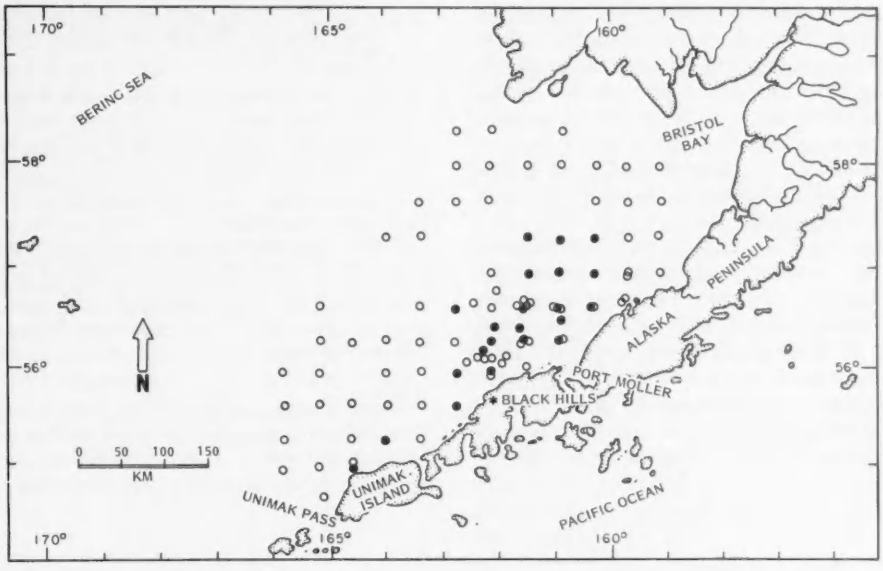

FIGURE 9.—Trawling stations (circles) in the southeastern Bering Sea where female king crabs were taken in May 1969 and 1970. Stations with crabs with empty egg cases are designated by solid circles.

distribution of egg-bearing king crabs with empty egg cases shown in Figure 9 was determined from trawling in May 1969 and 1970 (data combined). Weber (1967) also reported that in Bristol Bay, king crabs usually release their larvae in May.

RELATION BETWEEN DISTRIBUTION OF LARVAE AND CURRENT PATTERNS

My observations of the dispersal of stage I larvae from the release areas generally agree with the known patterns of water currents in the study area. Hebard (1959) found that in the southeastern Bering Sea water moved counterclockwise toward Bristol Bay along the Alaska Peninsula and away from Bristol Bay in the more northern parts of the southeastern Bering Sea. Under these conditions larvae released in the Black Hills-Port Moller area would be carried northeastward along the Alaska Peninsula toward the head of Bristol Bay. The seasonal shift of larvae shown in Figures 1 to 7 corresponds closely with this pattern of water movement.

Because of differences in water currents, the direction of seasonal shift of larvae is different in the Unimak Island area than it is to the east. Oceanographic studies in this area, summarized by Dodimead, Favorite, and Hirano (1963), show that water from the Gulf of Alaska flows northward through the interisland passages of the Aleutian Islands in the southeastern Bering Sea. Such a flow pattern through Unimak Pass is consistent with the apparent northward movement of king crab larvae from the Unimak Island area (Figure 3).

On the basis of his findings on water currents in the southeastern Bering Sea, Hebard (1959) postulated that recruitment of king crab larvae into the Bering Sea may occur through the island passages of the Aleutian Islands, especially Unimak Pass. If this is so, then the possibility exists that the stock of king crabs in Bristol Bay is derived to some extent from larvae released south of the Alaska Peninsula. Unfortunately, plankton was not collected south of Unimak Pass during the present study, and the question of recruitment of king crab larvae into Bristol Bay from areas south of the Alaska Peninsula must await a more detailed investigation.

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OCCURRENCE OF SILVER HAKE, *MERLUCCIUS BILINEARIS*, EGGS AND LARVAE ALONG THE MIDDLE ATLANTIC CONTINENTAL SHELF DURING 1966

MICHAEL P. FAHAY[1]

ABSTRACT

During an ichthyoplankton survey over the continental shelf between Martha's Vineyard, Mass. and Cape Lookout, N.C., from December 1965 to December 1966, 3,241 eggs and 11,032 larvae of the silver hake, *Merluccius bilinearis*, were collected. Eggs were collected from May until November, with a peak in June. Most of the eggs (77%) were collected south of Martha's Vineyard, Mass. The southernmost occurrence of eggs was off North Carolina in November. Larvae were collected from May until December, with a peak in September. Larvae were most abundant on the shelf between Hudson Canyon and Martha's Vineyard. The evidence suggests that most of the eggs and larvae collected on the survey had been spawned near the northeastern edge of the survey area and drifted southwesterly. There is also evidence of a size-related, diel, vertical migration by the postlarvae.

In December 1965, the Sandy Hook Marine Laboratory began a 1-yr ichthyoplankton survey of the continental shelf between Martha's Vineyard, Mass. and Cape Lookout, N.C. The survey was designed to delimit the spawning times and locations of marine game fishes, define dispersal patterns of larvae, and form the first phase in a study to determine what species depend on an estuarine environment during some phase of their early life history. We placed emphasis on no one species and began the survey with no preconceived notions on either the geographical extent or the seasonality of spawning of any species. This report on the eggs and larvae of silver hake, *Merluccius bilinearis* (Mitchill), represents one of a series resulting from that survey.

The silver hake is an important sport and commercial species widely distributed over the continental shelf of eastern North America from the Gulf of St. Lawrence (McKenzie and Scott, 1956) southward to South Carolina, with centers of abundance between Nova Scotia and New York (Bigelow and Schroeder, 1953). Silver hake are found in both shoal and deep water within a wide temperature range, usually over bottoms of sand or sand-silt mixtures (Fritz, 1965). When winter cooling occurs on the shelf, silver hake migrate to warmer waters on the continental edge and slope.

Silver hake in the western North Atlantic consist of two morphologically separable and nonmingling populations (Conover, Fritz, and Vieira, 1961) roughly separated by the 41°30′N meridian (Nichy, 1969). Hence, the Gulf of Maine and northern edge of Georges Bank contain one population, while the southern slopes of Georges Bank and continental shelf south and west of Cape Cod contain the other. This report concerns the eggs and larvae produced by the latter population.

Spawning in the Gulf of Maine extends from June to October, with a peak in July and August (Bigelow and Schroeder, 1953). Kuntz and Radcliffe (1917) described the embryological and larval development of silver hake and suggested that "the spawning period for this species is a protracted one and not all the eggs mature at one time." Sauskan and Serebryakov (1968), in a study of the gonads of silver hake from Georges Bank and the Nova Scotian shelf, showed: 1) larger females mature and spawn earlier than smaller ones; 2) vitellogenesis is asynchronous, and individual fish spawn in three portions within a season; 3) the initial spawning of an individual female accounts for half the total seasonal production of oocytes.

Silver hake eggs and larvae have been collected from Halifax, Nova Scotia to Cape May, N.J. (Bigelow and Schroeder, 1953). Eggs and larvae

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have been reported in local plankton collections as follows: off Nova Scotia (Dannevig, 1919); over Georges Bank (Marak and Colton, 1961); in Block Island Sound (Merriman and Sclar, 1952). Sauskan and Serebryakov (1968) discussed the distribution of silver hake eggs and larvae but limited their sampling and discussion to areas east of our 1966 sampling area.

MATERIALS AND METHODS

We conducted eight cruises aboard the RV *Dolphin* from December 1965 to December 1966. On each cruise, we sampled 92 stations arranged on 14 transects between Martha's Vineyard, Mass. and Cape Lookout, N.C. (Figure 1). The station arrangement allowed us to sample from nearshore to the 183-m (100-fathom) contour along each transect. We scheduled cruises to occur at 6-wk intervals, and the average cruise occupied 17 days. We sampled four transects from Martha's Vineyard to New Jersey on a supplemental cruise in September 1966. Dates and sampling sequences and locations of collecting stations listed to the nearest 0.8 km (0.5 nautical mile) are contained in Clark et al. (1969).

We used loran, radar and, where possible, visible ranges to position the *Dolphin* on station. Routine work on station involved the use of a bathythermograph to obtain temperature profiles, a stem thermometer to measure surface temperatures, and a Beckman[2] RS-5 portable salinometer to obtain salinities and temperatures from the surface to the maximum plankton sampling depth. In water deeper than the length of the salinometer cable, we used Frautschy water bottles and measured the salinities of these samples with a hydrometer kit. Temperature and salinity profiles resulting from the survey are found in Clark et al. (1969).

We chose the Gulf V high-speed plankton sampler (Arnold, 1959) to overcome many of the problems inherent in sampling ichthyoplankton. It samples at 5 knots, thus allowing capture of organisms capable of avoiding slower nets. Its large mouth opening provides large quantities of eggs and larvae per tow and, hence, samples with high reliability for comparative purposes. Flow-through characterisitcs of the net prevent extensive damage to larvae. Finally, the Gulf V is ruggedly built and requires a minimum of shipboard maintenance. Our sampler (Figure 2) consists of a conical net of 0.33-mm (0.013-inch) Monel wire with 12 meshes/cm (30 meshes/inch) and an

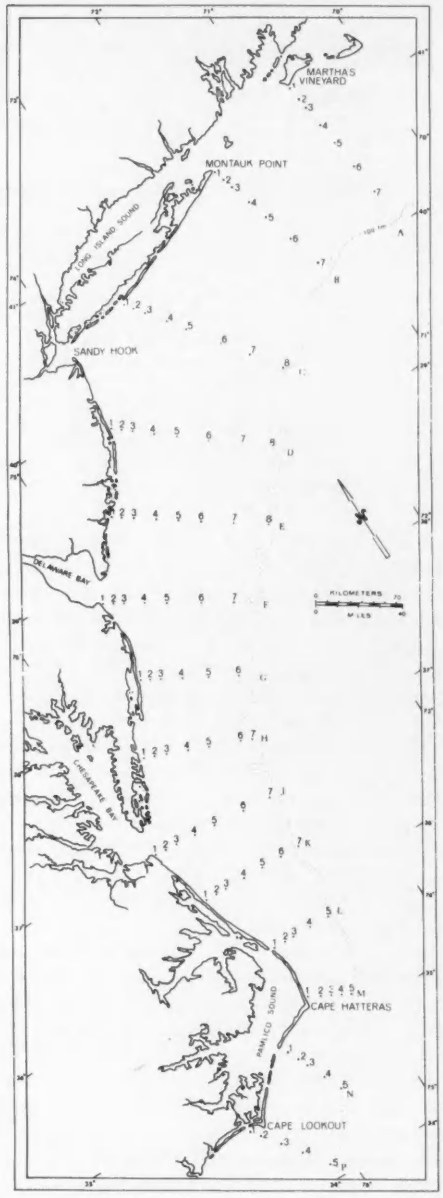

FIGURE 1.—RV *Dolphin* survey, December 1965 to December 1966. Location of transects and collecting stations.

[2]Reference to trade names does not imply endoresement by the National Marine Fisheries Service, NOAA.

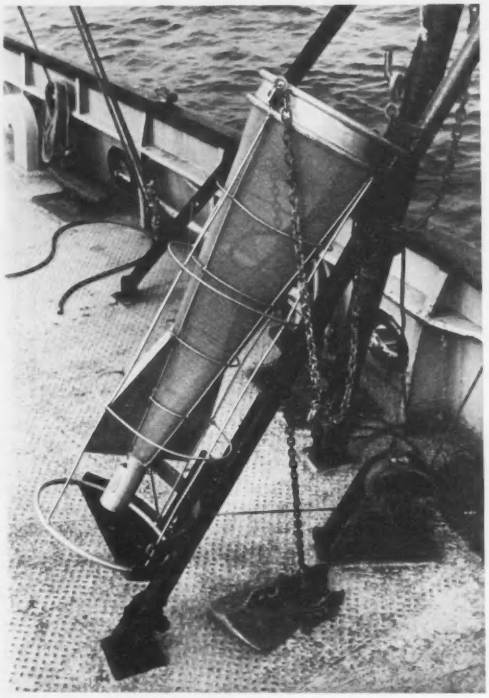

FIGURE 2.—Gulf V high-speed plankton sampler with depressor.

aperture size of 0.52 mm (0.02 inch). Other dimensions are as described by Arnold (1959).

Our method of towing two samplers consecutively was described in detail in Clark et al. (1969), Richards and Kendall (1973), and Smith (1973). Figure 3 illustrates schematically our towing methods over various depths of water. As illustrated in Figure 3, the step-oblique method sometimes resulted in unequal sampling intensity at certain depths under a unit of surface area. Therefore, to diagram the horizontal distribution on maps, I combined the catch of the two nets and adjusted them as shown in Table 1.

The catches of the two nets presented separately provide added useful information. This is especially true in view of 1) observed differences in numbers and length-frequencies between the catches of the two nets, and 2) the presence of a thermocline within the stratum sampled by the deep net. In Appendix Table 1, I tabulated the catch of the deep net as observed. However, the deep net was not equipped with a closing device and was subject to contamination in the upper 15 m during setting out and hauling back procedures. Therefore, for study of vertical distribution, I adjusted the deep net catch after assuming that it sampled the upper zone for 3 min.

Tows are labeled "D" (day), "N" (night), or "C" (crepuscular, i.e. within 1 h of sunrise or sunset) in Appendix Table 1.

After each tow, we washed the samplers down, removed the cups, and preserved the samples in buffered 5% Formalin. The samples were returned to the laboratory where all ichthyoplankton was removed and larvae divided into family groups. Gadids and merlucciids were then identified to species. Eggs were initially grouped according to their diameters. Early silver hake eggs are indistinguishable from the eggs of many other species of marine fishes. Common characteristics include: outside diameter of about 1.0 mm, presence of a single oil globule, narrow perivitelline space, and 4:1 ratio of egg diameter to oil globule diameter. Consequently, specific identifications were limited to eggs in advanced stages of development. I based identifications of late stage *M. bilinearis* eggs on published descriptions (Kuntz and Radcliffe, 1917; Sauskan and Serebryakov, 1968) and on my own rearing experiments with artifically fertilized eggs. The purpose of my experiment was to determine whether pigment was present on the yolk. It was terminated before hatching occurred. Prolarval offshore hake, *M. albidus*, were identified following the descriptions by Marak (1967) and removed from the *M. bilinearis*

TABLE 1.—Method used to combine the catches of shallow and deep samplers.

Shallow net		Deep net		
Number of steps	Minutes per step	Number of steps	Minutes per step	Total station catch formula
2	15	0	0	⅓ shallow
3	10	0	0	½ shallow
6	5	0	0	Total shallow
6	5	2	15	Total shallow + ⅓ deep
6	5	3	10	Total shallow + ½ deep
6	5	6	5	Total shallow + total deep

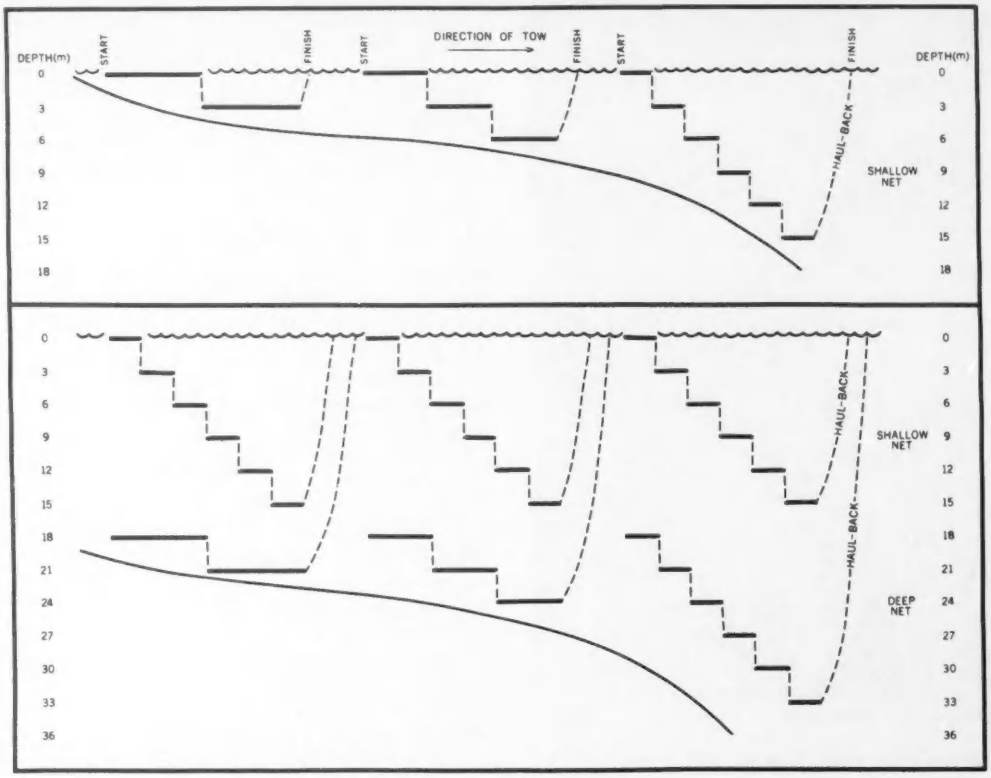

FIGURE 3.—Six sampling methods for ½-h plankton tows over different water depths.

collection. I also removed several postlarvae recognized as *Merluccius* sp. but which I presume are *M. albidus*, the postlarvae of which are undescribed.

We measured all specimens, except mutilated ones, from the tip of the snout to the tip of the notochord or urostyle with an ocular micrometer or point-to-point dial calipers. Measurements are expressed as millimeters notochord length (mm NL) and recorded to the nearest 0.1 mm. Because preservation resulted in shrinkage of specimens, the recorded size of some larvae is smaller than the reported hatching length of 2.8 mm (Kuntz and Radcliffe, 1917).

RESULTS

Egg and larval distributions are shown in Appendix Table 1 and Figures 4 through 8. A map is not shown for the one egg and one larva caught off the Virginia coast on May 20 and 22, respectively.

Distribution of Eggs

Eggs identified as silver hake for this report are in stages III and IV of development, when the embryo encompasses at least 75% of the yolk and the tail tip is separated from the yolk surface. Fine pigment is present on the part of the yolk surface lying under the snout of the embryo. This is not shown by Kuntz and Radcliffe (1917).

We collected 3,241 silver hake eggs from May through November 1966, with a peak in June. The temporal distribution of eggs changed geographically. Spawning began earlier in the northeastern end of our survey area and progressively later to the south. Table 2 demonstrates this trend for four transect groups. According to Sauskan and Serebryakov (1968), about half the total seasonal

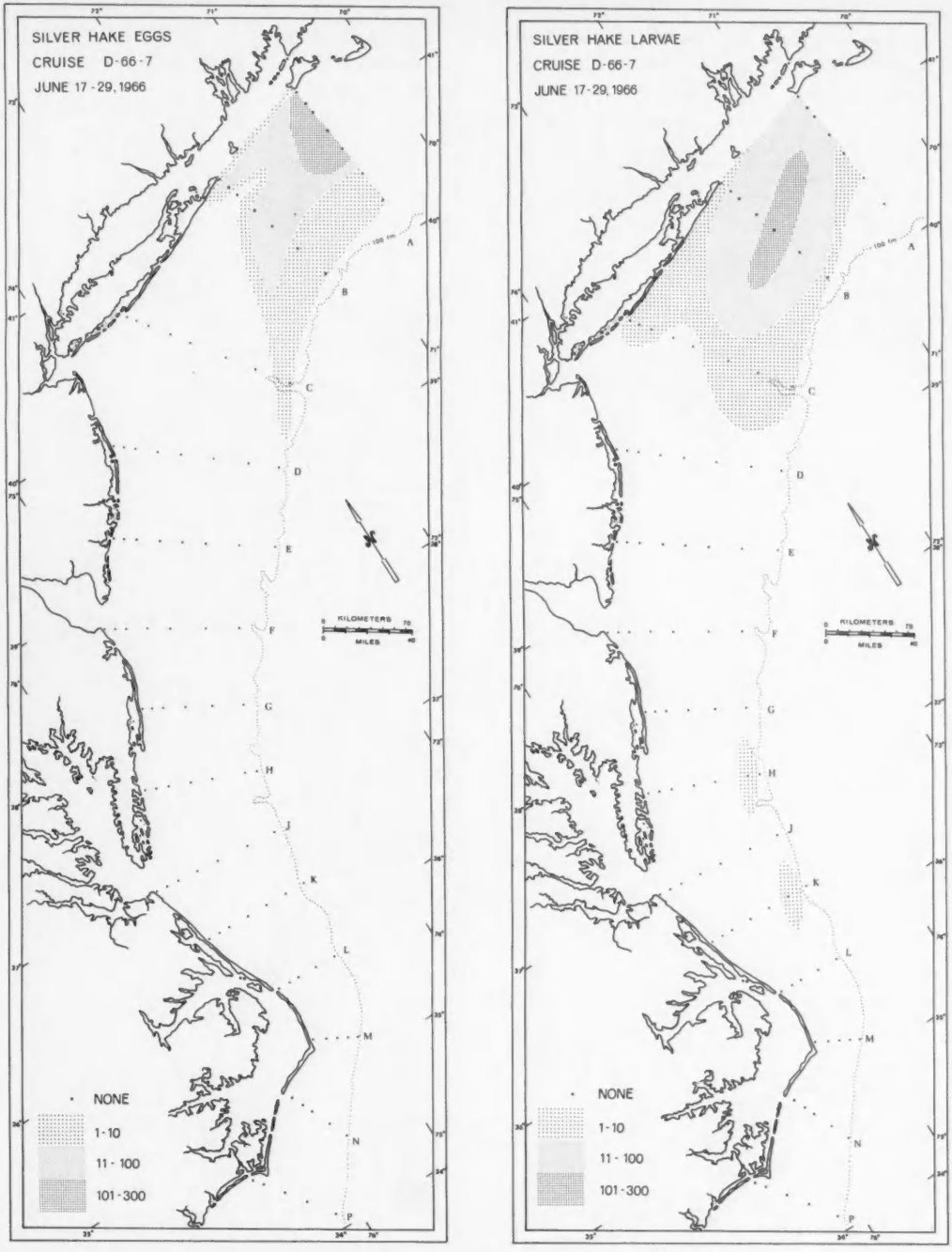

FIGURE 4.—Occurrence of silver hake eggs and larvae, June 1966.

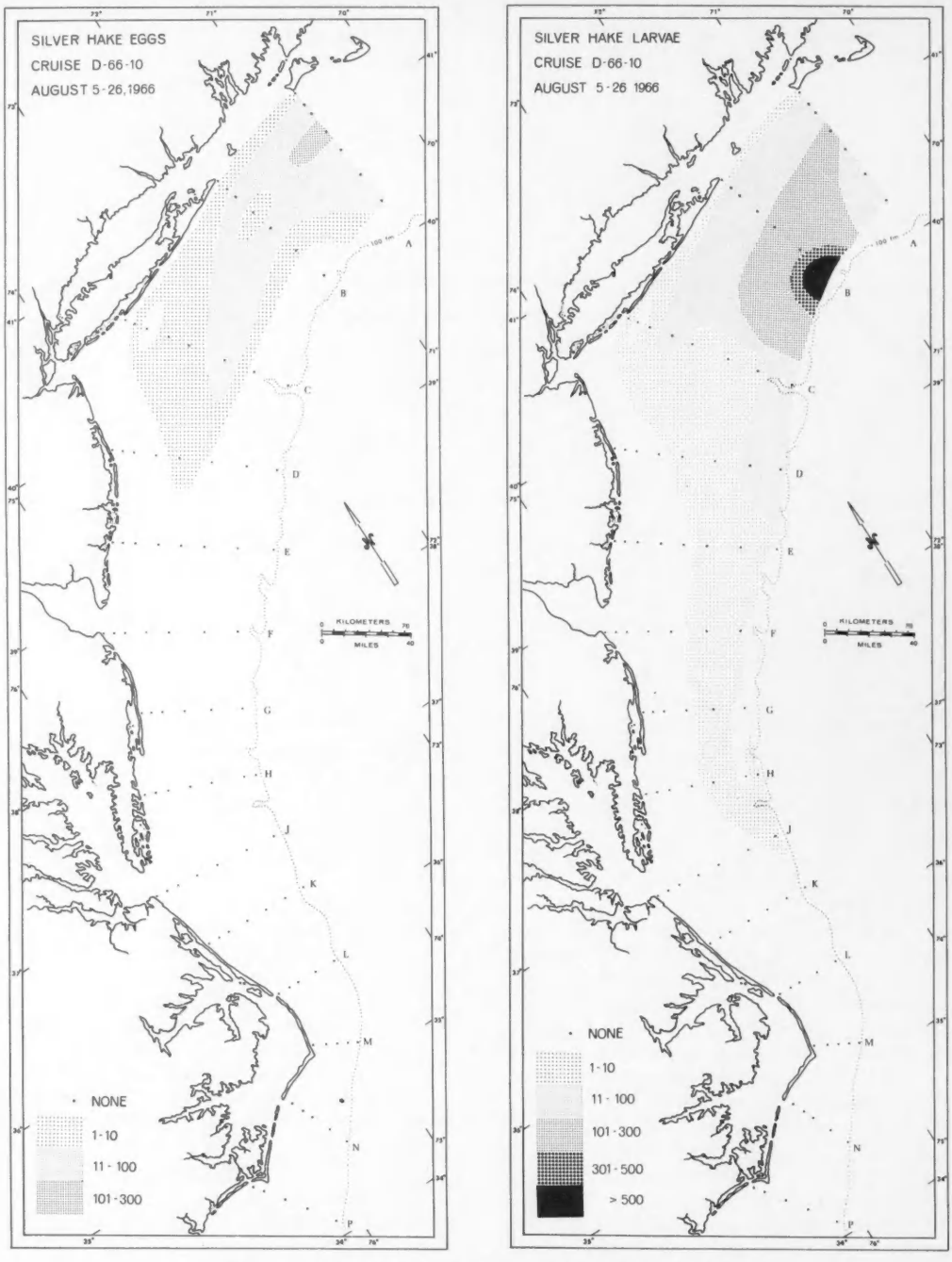

FIGURE 5.—Occurrence of silver hake eggs and larvae, August 1966.

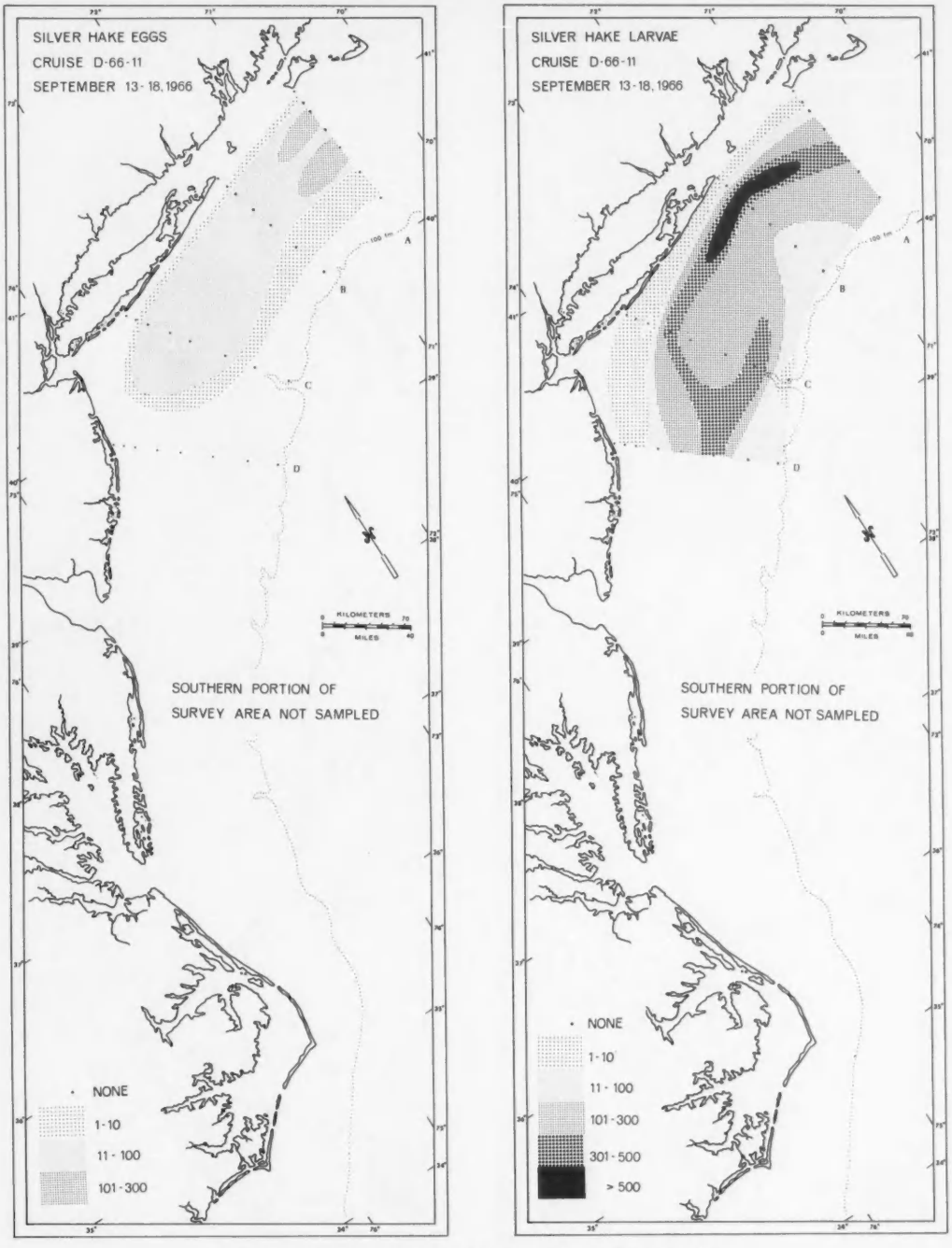

FIGURE 6.—Occurrence of silver hake eggs and larvae, September 1966.

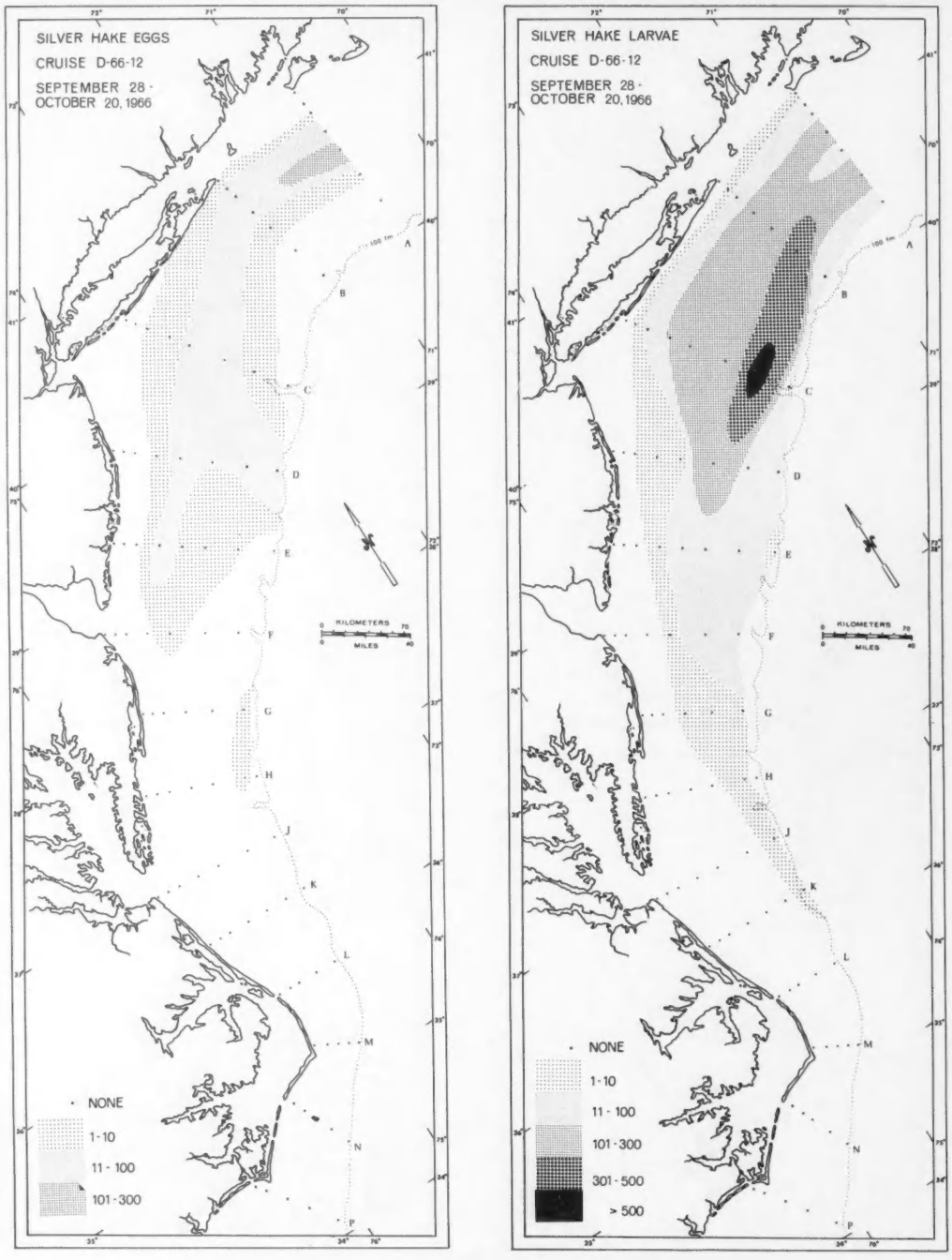

FIGURE 7.—Occurrence of silver hake eggs and larvae, September-October 1966.

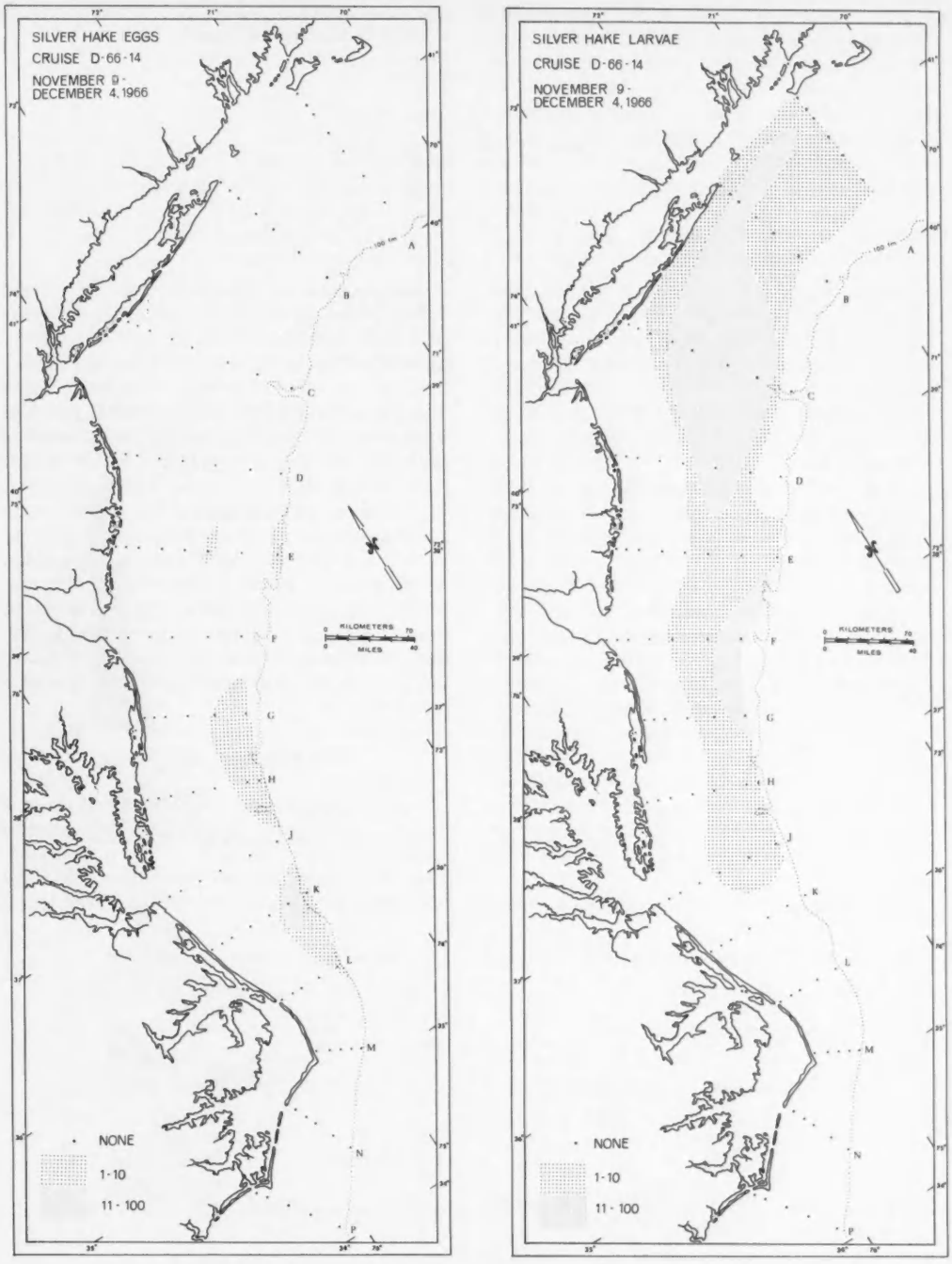

FIGURE 8.—Occurrence of silver hake eggs and larvae, November-December 1966.

TABLE 2.—Monthly distributions of silver hake eggs arranged by transect-groups. Monthly peak abundance for each group indicated by bold type. ns = not sampled.

Transect groups	Numbers of eggs collected						
	May	June	Aug.	Sept.	Oct.	Nov.-Dec.	Total
AB	0	**1,362**	415	617	454	0	2,848
C	0	5	26	**108**	48	0	187
DEF	0	0	6	0	**141**	9	156
GHJKL	1	1	0	ns	3	**45**	50
Total	1	1,368	447	725	646	54	3,241

production of eggs is released in a first batch, and the second half is divided between second and third batches. Our egg collections on the shelf south of Montauk Point and Martha's Vineyard (transects A and B in Table 2) are consistent with their conclusion. We collected 1,362 eggs in June, the remainder during August (415), September (617), and October (454).

The silver hake eggs collected during our 1966 cruises originated principally over Nantucket Shoals and on the continental shelf south of Martha's Vineyard. We collected 88% of the eggs on the two northernmost transects, 77% on the Martha's Vineyard transect alone. Sauskan and Serebryakov (1968) found concentrations south of Martha's Vineyard in May, on the southern slopes of Georges Bank in June. Thus, this area probably is an important silver hake spawning center. Small, distinct spawning groups are also located near Hudson Canyon, on the deeper parts of the shelf off New Jersey, and further south off Delaware, Maryland, and Virginia. The small numbers of eggs collected in the latter areas probably reflect the small numbers of adults occurring there.

Silver hake eggs are found in as wide a range of temperatures as the adults. The relation between numbers of eggs collected and surface temperatures is shown in Table 3. This may be misleading however, for we observed egg concentrations in a particular geographic area (south of Martha's Vineyard and Montauk Point) and these concentrations were apparently independent of prevailing surface temperatures which ranged from 13.5° to 21.7°C. It is not known how near the bottom silver hake spawn, nor in what range of temperatures. Assuming they spawn near the bottom, the wide temperature range of egg occurrences might be due to a wide range of temperatures in the spawning areas or might simply be the result of extreme temperature ranges in surface waters over the spawning areas, in which case the ascending eggs demonstrate a wide temperature tolerance.

Distribution of Larvae

Larval distributions are shown in Appendix Table 1 and Figures 4 through 8. We collected 11,032 silver hake larvae from May to December 1966, 91% during August, September, and October (Table 4). We captured no postlarvae larger

TABLE 3.—Abundance of silver hake eggs relative to observed surface temperatures.

Surface temperature (°C)	Number of tows which collected:				Total number of tows
	1-10 eggs	11-100 eggs	101-200 eggs	200+ eggs	
10.0-10.9	1				1
11.0-11.9	1				1
13.0-13.9	5			1	6
14.0-14.9	16	6	3	3	28
15.0-15.9	14	6	1		21
16.0-16.9	13	2			15
17.0-17.9	9	3	3		15
18.0-18.9	3	4	1		8
19.0-19.9	4	4			8
20.0-20.9	6	5			11
21.0-21.9	7	2			9
22.0-22.9	1				1
Total tows	80	32	8	4	124

TABLE 4.—Numbers of silver hake larvae collected during six cruises in 1966.

May	June	Aug.	Sept.	Oct.	Nov.-Dec.	Total
2	585	2,989	3,875	3,175	406	11,032

than 18.0 mm NL until the August cruise (Figure 9). Since the spawning season probably began in early June, and since 18.0 mm approximates the size at which silver hake postlarvae begin to live near the bottom, the length of pelagic life is apparently about 2 mo.

Within our 1966 sampling area, larvae were most densely concentrated between Nantucket Shoals and Hudson Canyon. Progressing southward, we found larvae increasingly restricted to the offshore part of the shelf. Distribution varied according to the size of larvae. Generally, we found smaller larvae inshore and near the surface, and larger larvae offshore and deeper. Smaller larvae were also more numerous in the northeastern part of the survey area than the southwestern. Tables 5 through 7 illustrate this trend for the August, September, and October cruises. These differences in distribution by size are partly a result of a southwesterly drift during growth, partly a preference by larger larvae for deeper water.

Silver hake larvae in 1966 were distributed in areas where surface temperatures ranged from 8.6° to 25.8°C. Since silver hake larvae are not necessarily surface-dwelling animals, the mean observed temperatures within the depths sampled by the two Gulf V nets may be more significant. Table 8 shows the number of tows containing larvae (arranged by volume of catch) relative to these temperatures. The total number of tows, regardless of the presence of silver hake, is in-

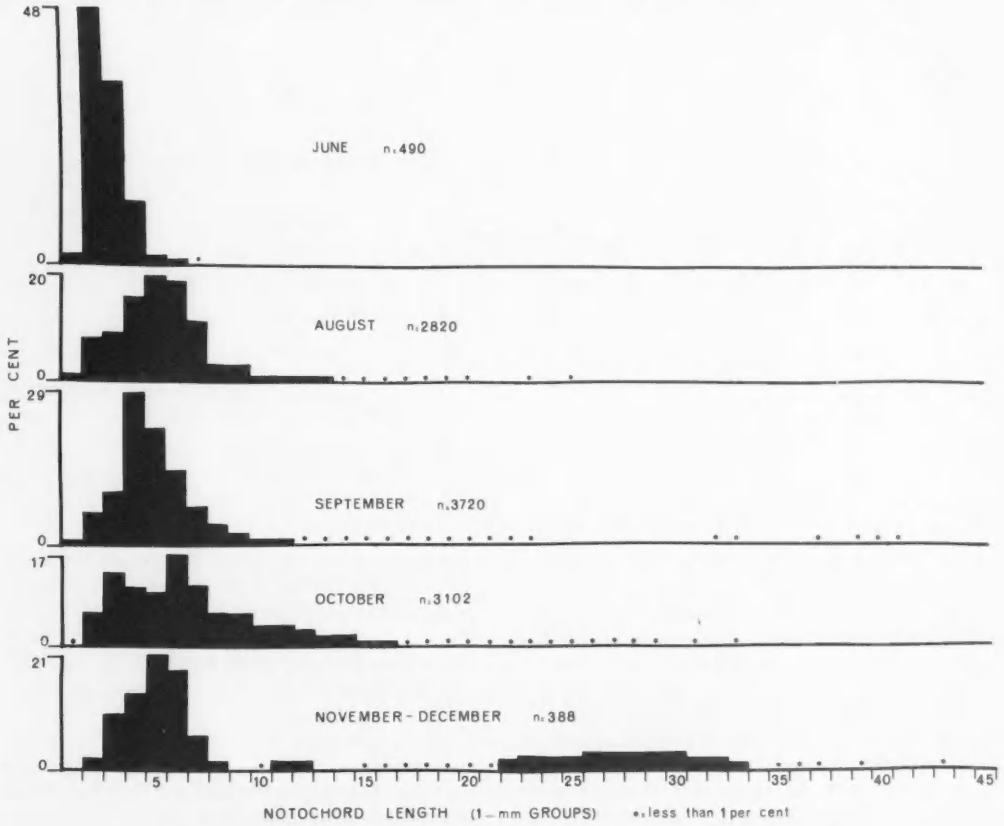

FIGURE 9.—Length-frequency distributions of silver hake larvae during five cruises, 1966.

TABLE 5.—Mean lengths (mm NL) of silver hake larvae collected during *Dolphin* cruise D-66-10 (August 1966), arranged by transect, net 1 (0-15 m) or net 2 (18-33 m), and station.

Transect	Net	Station 1	2	3	4	5	6	7	8	Mean length	*N*
A	1	3.2	2.8	4.0	3.1	5.0	4.0	3.6		3.8	598
	2			5.8	5.1	5.3	5.8	4.2		5.6	658
B	1	2.6	3.8	2.0	3.9	4.1	5.4	6.6		5.4	413
	2		3.6	3.3	5.5	6.2	6.8	8.5		7.8	1,037
C	1	2.1		3.2	3.6		3.2		4.9	3.5	54
	2				4.7	3.5		5.3	5.4	5.3	98
D	1					3.8	5.8	6.0	3.6	5.6	33
	2					3.2		12.2	10.2	10.3	71
E	1						5.3	3.3		4.0	3
	2						6.0	5.5		5.7	8
F	1						6.0	7.5		7.3	8
	2						7.0			7.0	2
G	1					3.6				3.6	1
	2										
H	1					14.8				14.8	1
	2					14.5		15.1		15.0	3
J	1										
	2							5.7		5.7	1
Mean length		3.0	3.2	4.2	3.6	5.1	5.6	7.9	7.4	6.1	
N		18	67	82	357	472	853	987	153		2,989

TABLE 6.—Mean lengths (mm NL) of silver hake larvae collected during *Dolphin* cruise D-66-11 (September, 1966), arranged by transect, net 1 (0-15 m) or net 2 (18-33 m), and station.

Transect	Net	Station 1	2	3	4	5	6	7	8	Mean length	*N*
A	1		3.0	3.6	4.2	4.5	5.8	5.0		4.7	478
	2		3.0	3.9	3.8	4.8	5.9	5.2		4.9	529
B	1	2.7	2.8	4.2	3.5	5.6	7.0	11.6		4.8	79
	2			5.6	4.9	4.1	6.6	12.0		5.7	921
C	1	3.0	2.7		4.4	3.0		12.3	8.2	7.2	29
	2				4.2	6.9	5.6	8.5	9.7	6.4	1,011
D	1		3.6	2.8	3.4	3.8	6.0	8.8		4.5	62
	2				2.8	4.9	5.5	7.0	9.1	5.8	620
Mean length		2.8	2.9	5.4	4.3	5.0	5.7	7.9	9.1	5.6	
N		14	22	615	730	799	840	650	59		3,729

cluded in the table to demonstrate the possibility that the temperature relationship is simply an artifact created by our cruise schedule. The probability of collecting these temperature-tolerant larvae at any temperature increases as sampling at that temperature increases.

Our maximum sampling depth was below the thermocline on all stations where we captured larval silver hake. Larvae apparently were more concentrated near the thermocline than near the surface during the summer months. Table 9 compares the percentage of the total catch contributed by the deep net (which sampled near the thermocline) during each cruise with observed surface temperatures and indicates that during August and September, when surface temperatures were highest, silver hake larvae were distributed more deeply where temperatures were lower.

Our cruise schedule and sampling sequence resulted in many consecutive stations being sampled during the same light regime. Thus, opportunities for comparing the diel differences in the captures of silver hake larvae are limited.

TABLE 7.—Mean lengths (mm NL) of silver hake larvae collected during *Dolphin* cruise D-66-12 (October, 1966), arranged by transect, net 1 (0-15 m) or net 2 (18-33 m), and station.

Transect	Net	Station 1	2	3	4	5	6	7	8	Mean length	*N*
A	1	3.4	4.2	4.7	3.5	3.1	5.5	9.9		3.8	143
	2		4.1	4.9	3.5	3.0	4.7	13.5		4.7	554
B	1		2.8	3.3	5.8	9.6	10.2	11.2		9.7	77
	2		5.5	4.4	6.4	7.5	10.8	9.6		8.7	699
C	1		8.7	7.1	5.8	5.0	7.6	13.5	19.8	8.3	157
	2			5.6	6.7	6.0	7.8	9.9	12.8	8.6	825
D	1	2.7		7.1		6.2	6.2	4.2	2.9	5.6	172
	2				15.0	6.1	6.9	5.6	4.5	6.3	212
E	1				2.8	6.4	6.6	8.0	3.5	6.4	67
	2					5.1	8.5	10.0	3.0	8.7	87
F	1					5.6	6.5	4.7		6.3	70
	2					3.7	7.0	6.3		6.4	27
G	1				5.4					5.4	1
	2					4.6	7.4			5.5	3
H	1										
	2						15.0			15.0	1
J	1										
	2							22.5		22.5	1
K	1							11.0		11.0	1
	2										
Mean length		3.2	4.5	5.1	4.8	6.2	7.7	9.6	4.8	7.3	
N		3	53	84	560	536	1,001	816	44		3,097

TABLE 8.—Abundance of silver hake larvae relative to mean temperature within the sampling depths of individual Gulf V nets.

Temperature (°C) within samplers' depth range	Number of tows which collected: 1-10 larvae	11-100 larvae	101-300 larvae	301-500 larvae	500+ larvae	Number of tows: Containing silver hake	Total
6.0-6.9	5	2				7	9
7.0-7.9	3					3	12
8.0-8.9	4	2		1		7	18
9.0-9.9	17	2				19	34
10.0-10.9	9	8	2			19	32
11.0-11.9	5	5				10	17
12.0-12.9	4	6	3	2		15	22
13.0-13.9	14	7	3	1		25	48
14.0-14.9	22	14	8		2	46	75
15.0-15.9	8	8	2	1		19	38
16.0-16.9	12	6	1			19	36
17.0-17.9	12	5	2			19	44
18.0-18.9	4	6				10	33
19.0-19.9	1	5	4			10	39
20.0-20.9	8	3	1			12	23
21.0-21.9	6	1	1			8	25
22.0-22.9	6					6	29
23.0-23.9	1					1	14
24.0-24.9	1					1	20
25.0-25.9						0	11
26.0-26.9						0	6
Total tows	142	80	27	5	2	256	

Although day and night tows were equally productive (Table 10), differences exist when larval size is considered. Most of the smallest larvae were taken during the day, while most larger larvae and postlarvae were taken from dusk to dawn (Figure 10).

There are several possible explanations for the higher incidence of larger larvae and postlarvae

TABLE 9.—Contribution of deep net to total catch of larvae on stations where both nets were used, compared to weighted mean surface temperature.

Cruise	Month	Percent caught in deep net	Weighted mean surface temperature (°C)	Total number caught in both nets
D-66- 5	May	0	14.4	1
D-66- 7	June	34	14.5	408
D-66-10	Aug.	62	20.6	2,940
D-66-11	Sept.	82	19.9	3,836
D-66-12	Oct.	78	15.5	3,164
D-66-14	Nov.-Dec.	52	11.7	398

TABLE 10.—Diel differences in captures of silver hake larvae, cruises D-66-7 (June) through D-66-14 (November-December).

Light regime	Number of tows		Number of larvae	Weighted mean length (mm NL)	Average catch	
	Total	Containing silver hake			Total tows	Tows containing silver hake
Dawn	62	21	810	5.4	13.1	38.6
Day	265	112	4,741	5.3	17.9	42.3
Dusk	48	18	1,255	5.7	26.1	69.7
Night	240	104	4,226	7.8	17.6	40.6

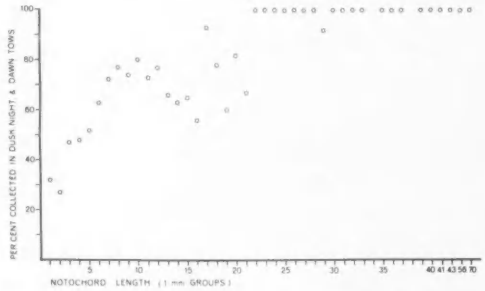

FIGURE 10.—Percentage of silver hake larvae collected in non-day tows per 1-mm size groups.

in night tows, the most generally accepted being that larvae avoid the approaching sampler during daylight in response to visual warning. The difference cannot be attributed to vibration of the towing cable or inefficient filtration by the sampler because these factors are equal during all light regimes. Undersampling of larger larvae of other species during daylight has been well documented (Silliman, 1943; Bridger, 1956; Ahlstrom, 1959; Colton, 1965). These authors, however, noted diel differences resulting from tows made at 1 knot. Miller, Colton, and Marak (1963) towed a high-speed plankton sampler at 7 knots and found no significant differences in the day and night catches of haddock larvae and pelagic juveniles. Ryland (1963) concluded that a towing speed of 5 knots (257.4 cm/s) was sufficient to prevent net avoidance by plaice larvae up to 20.0 mm whose maximum "darting velocity" he found to be 20 cm/s. If, by towing at 5 knots, we were able to overcome net avoidance by larger larvae, then the presence of larger larvae in night tows only must reflect some form of diel activity or vertical migration. Kelly and Barker (1961) found a significant difference in depth distribution with growth of young redfish, the larger juveniles occurring in deeper layers. A similar difference plus a diel change in depth distribution is observed with silver hake when the light regime, capture depth (net 1 vs. net 2), and mean larval length are combined (Figure 11). The largest larvae were captured in the deep net during the night, the smallest larvae in the shallow net during the day. In both nets, night tows contained larger larvae than day tows, and in both light regimes the deep net contained larger larvae than the shallow net. Evidently, with growth, silver hake larvae seek deeper water, perhaps in response to increasing negative phototropism, perhaps simply approximating the adult habitat.

During the summer of 1970, we made two cruises to investigate the size at which silver hake larvae first occur on or near bottom. On 12 stations northeast and southwest of Hudson Canyon, we made reciprocal tows with Gulf V samplers and an otter trawl (39-foot headrope) fitted with a ¼-inch mesh cover bag and separate cod end. Length frequencies of the Gulf V catches, compared with those of the otter trawl (Figure 12), indicate that silver hake first become available to bottom

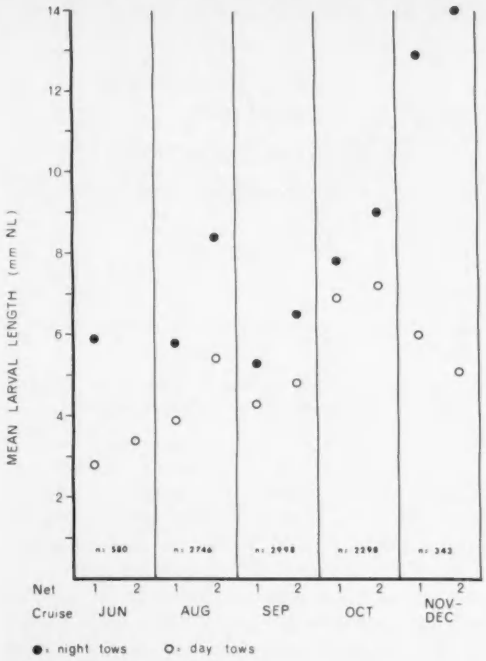

FIGURE 11.—Comparisons of silver hake mean larval size, light condition, and depth of capture. Net 1 sampled to a maximum of 15 m; net 2 to a maximum of 33 m.

sampling gear at about 17.0 to 20.0 mm NL. This figure is somewhat smaller than that indicated by Nichy (1969), whose smallest specimens taken by otter trawl were about 50 mm.

During 1966, all postlarvae larger than 21.0 mm NL (except one) were captured at night, and most of those were taken in the deep net, which sampled above, within, and below the thermocline, if one was present. Postlarvae larger than 21.0 mm NL were taken in the shallow net only when the thermocline was weak or nonexistent. All this suggests that silver hake postlarvae seek the bottom at about 17.0 to 20.0 mm NL and migrate vertically at night, ascending at least to the thermocline depth or, in the absence of a thermocline, to levels nearer the surface.

DISCUSSION

The area encompassing the southern slope of Georges Bank, Great South Channel, Nantucket Shoals, and the shelf south of Martha's Vineyard is evidently an important spawning center for silver hake. Unfortunately, neither the *Dolphin* survey nor the Soviet surveys (Sauskan and Serebryakov, 1968) sampled this area extensively enough to determine all the possible drift patterns of eggs and larvae. The 70°40'W meridian approximates the eastern limit of the *Dolphin* survey and the western limit of the sampling reported by Sauskan and Serebryakov.

Within this wide area, eggs should be expected to drift in several different directions, depending on the location of spawning and on long-term prevailing winds. One component of the westerly current on the shelf south of Martha's Vineyard and Nantucket Island originates on the southern slope of Georges Bank where it forms the southern part of a rotational eddy (Bigelow, 1927; Klimenkov and Pakhorukov, 1963; Bumpus and Chase, 1965; Bumpus and Lauzier, 1965; Harrison et al., 1967). Eggs spawned on Georges Bank may 1) drift with the eddy, develop, and recruit back to Georges Bank, or 2) drift west and south of Martha's Vineyard where we consistently found concentrations. Walford (1938) described similar patterns for haddock larvae spawned on Georges Bank. A third possibility may result in the loss of the brood. Colton (1959) reported that silver hake larvae spawned on Georges Bank were killed when a southerly drift carried them off the bank and into warm slope water (the rate of warming exceeding the larvae's rate of acclimation). Presumably, in addition to the perils of warming waters, silver hake larvae carried off Georges Bank into the slope water or Gulf Stream would be carried to the east and, unable to find suitable depths in which to begin the demersal stage, would perish.

Eggs spawned south of Martha's Vineyard drift west but probably not far before hatching, for the incubation period is only 48 h (Kuntz and Radcliffe, 1917). Unfortunately, these authors did not cite the temperature at which incubation or hatching occurred. If we assume (as did Sauskan and Serebryakov, 1968) that Kuntz and Radcliffe incubated their eggs at a maximum temperature of 20°C, then the maximum incubation period in degree-hours would be 960 ($48 \times 20 = 960$). We encountered the heaviest concentrations of eggs on the Martha's Vineyard transect when surface temperatures ranged from 13° to 22°C. Even at the minimum temperature of 13°C, incubation would occupy no more than 73.8 h ($960/13 = 73.8$). Currents between Georges Bank and Delaware

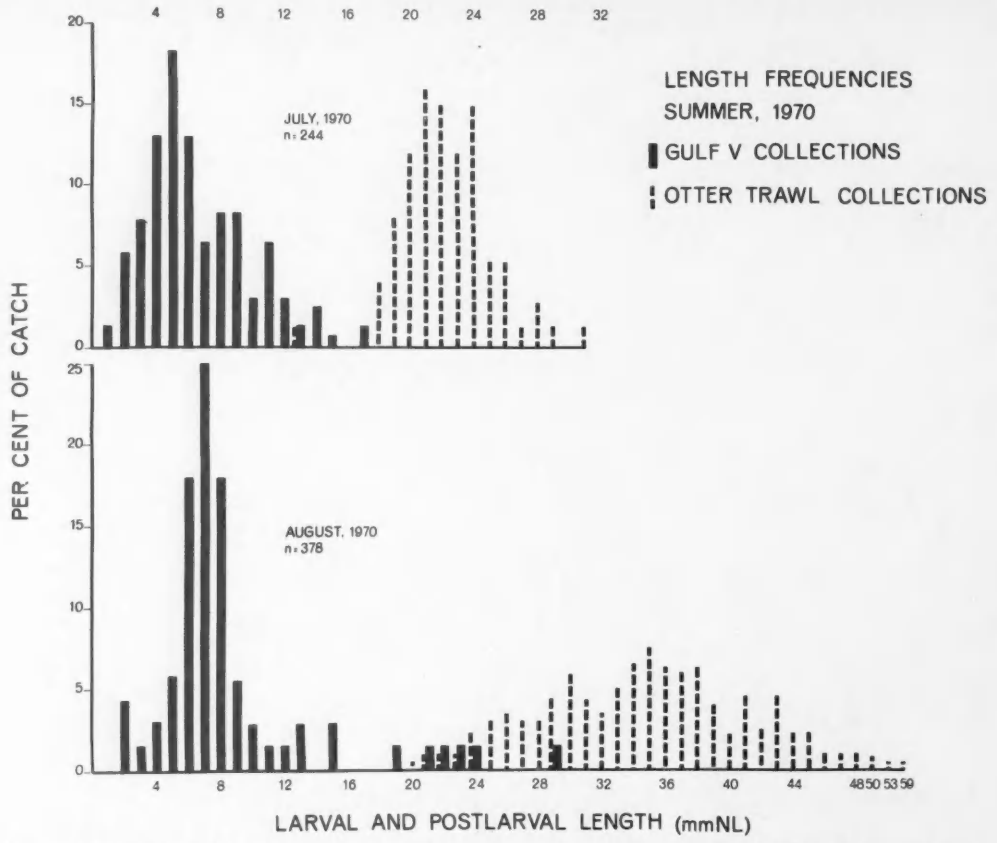

FIGURE 12.—Comparison of length frequencies of silver hake larvae and post-larvae captured in Gulf V plankton samplers near surface and otter trawl on bottom during summer cruises, 1970.

Bay flow west to southwest at average speeds of 0.93 km/h over the shelf between Nantucket Shoals and New Jersey (U.S. Navy Hydrographic Office, 1965) to 1.04 km/h over the southeast slope of Georges Bank (Sauskan and Serebryakov, 1968). Thus, the maximum distance an egg would drift from spawning to hatching is 76.8 km ($1.04 \times 73.8 = 76.8$) in the area of greatest egg abundance which we observed. This is substantiated by the fact that the center of abundance of the prolarvae is only slightly further to the southwest than that of the eggs. Also contributing to the short drift of eggs and prolarvae is the sluggish, meandering nature of currents on the shelf south of New England. During the summer of 1971, while studying vertical distribution of silver hake larvae on the shelf south of Montauk Point, we deployed a free-drifting staff buoy and sampled around it for 48 h. The course of the buoy (Figure 13) demonstrates the capriciousness of surface currents in the area, while indicating a net westerly drift.

I consider the silver hake eggs and larvae which we collected to be 1) representatives of a small brood spawned on the deeper portions of the shelf between Hudson Canyon and Cape Hatteras; 2) representatives of a brood spawned over Nantucket Shoals and the shelf south of New England; 3) survivors of a brood spawned over Georges Bank or Great South Channel.

It is during the pelagic period of development that eggs or larvae, unable to control their own movements, are most susceptible to prevailing currents, surface winds, and changing hydro-

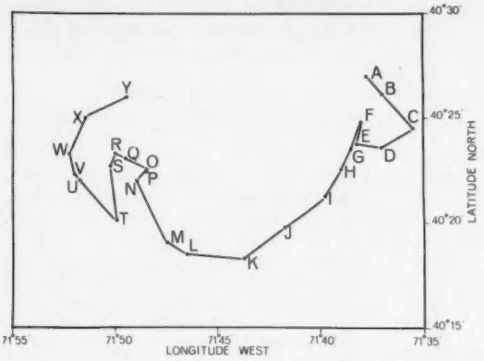

FIGURE 13.—Position of free-drifting staff buoy at 2-h intervals on the continental shelf south of Montauk Point, N.Y.

graphic conditions. The results of the *Dolphin* survey indicate several things about sampling fishes during this phase in their development. 1) One cannot hope to fully understand the early life history of any one species of fish on exploratory surveys. Such facts as gross seasonality and geographic limits of spawning might be revealed but a complete evaluation of a species' early life history can only follow a series of frequent cruises where all efforts are focused on one or a very few species. 2) Known or suspected zoogeographic barriers should be included well within the limits of a survey area, not made to coincide with the edge. 3) Sampling between the surface and levels immediately below the thermocline is inadequate when dealing with pelagic young of groundfish. A more complete and accurate picture of developing silver hake could have been drawn if the entire water column, surface to bottom, had been sampled on all stations. 4) The diel activity and vertical distribution of a postlarval fish may be directly related to the behavior of invertebrate food organisms. An analysis of the invertebrate plankton collected with the ichthyoplankton should be considered as an integral part of a survey. 5) Unless discrete-level tows are made with opening-closing nets, an exact temperature-catch relationship cannot be determined, except in vertically isothermal conditions.

I found no evidence that silver hake depend on or utilize estuaries during their early life history. Their occasional presence in estuarine areas must be considered accidental.

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APPENDIX TABLE 1.—Silver hake: station data, number of eggs, and number and length range of larvae collected during 1966.

Cruise and station	Net	Date	Start time	Depth of water (m)	Maximum tow depth (m)	Light regime[1]	Total number of eggs	Larvae			
								Total number captured	Number measured	Notochord length	
										Mean (mm)	Range (mm)
D-66-5			EDST								
B-1	1	13 V 66	2233	24-20	6	N	—	1	1	71.20	71.2
H-5	2	20 V 66	0527	24-40	24	C	1	—	—	—	—
K-5	1	22 V 66	0533	33-35	15	C	—	1	1	2.50	2.5
D-66-7			EDST								
A-1	1	17 VI 66	0927	11-27	6	D	206	81	54	2.40	1.7-2.8
A-2	1	17 VI 66	1037	29-37	15	D	242	75	55	2.28	1.8-3.2
A-3	1	17 VI 66	1137	29-48	15	D	117	49	35	2.21	1.8-2.6
A-3	2	17 VI 66	1137	29-48	24	D	209	3	3	2.10	1.9-2.3
A-4	1	17 VI 66	1322	51-53	15	D	107	3	3	3.33	3.2-3.6
A-4	2	17 VI 66	1322	51-53	33	D	158	16	15	2.43	2.0-3.1
A-5	1	17 VI 66	1703	62-62	15	D	123	4	3	2.70	2.2-3.1
A-5	2	17 VI 66	1703	62-62	33	D	79	1	1	2.80	2.8
A-6	1	17 VI 66	1919	73-75	15	C	1	—	—	—	—
A-7	1	17 VI 66	2343	117-102	15	N	1	—	—	—	—
B-1	1	18 VI 66	1732	24-24	15	D	4	3	3	2.77	2.5-3.3
B-2	1	18 VI 66	1622	46-42	15	D	16	18	16	2.61	2.0-5.3
B-2	2	18 VI 66	1622	46-42	24	D	3	—	—	—	—
B-3	1	18 VI 66	1525	53-51	15	D	—	15	15	2.95	2.1-4.4
B-3	2	18 VI 66	1525	53-51	33	D	—	4	4	2.55	2.4-2.8
B-4	1	18 VI 66	1402	62-64	15	D	20	15	14	3.34	2.8-4.1
B-4	2	18 VI 66	1402	62-64	33	D	7	6	3	3.63	2.7-5.0
B-5	1	18 VI 66	1036	77-75	15	D	1	120	116	3.33	2.4-5.7
B-5	2	18 VI 66	1036	77-75	33	D	64	62	56	3.33	2.4-4.7
B-6	1	18 VI 66	0833	86-86	15	D	—	24	24	3.93	2.7-4.6
B-6	2	18 VI 66	0833	86-86	33	D	3	60	60	3.65	2.9-4.4
B-7	1	18 VI 66	0412	88-99	15	C	—	1	1	3.10	3.1
B-7	2	18 VI 66	0412	88-99	33	C	1	—	—	—	—
C-1	1	19 VI 66	0628	20-29	15	D	—	8	2	3.60	2.7-4.5
C-2	2	19 VI 66	0733	31-31	27	D	—	1	1	2.90	2.9
C-3	1	19 VI 66	0827	35-37	15	D	—	2	2	4.15	4.1-4.2
C-6	1	19 VI 66	1531	58-58	15	D	—	1	1	5.20	5.2
C-6	2	19 VI 66	1531	58-58	33	D	—	5	5	5.74	5.1-6.3
C-7	1	19 VI 66	2043	79-77	15	C	—	4	3	6.30	5.8-6.9
C-8	1	19 VI 66	2310	112-320	15	N	4	2	2	4.90	4.7-5.1
C-8	2	19 VI 66	2310	112-320	33	N	1	—	—	—	—
H-6	1	27 VI 66	0654	79-97	15	D	—	1	1	6.30	6.3
H-7	2	27 VI 66	0758	102-214	33	D	1	—	—	—	—
K-6	1	25 VI 66	2205	42-49	15	N	—	1	1	7.80	7.8
D-66-10			EDST								
A-1	1	5 VIII 66	0502	9-22	6	C	1	14	13	3.15	2.2-5.6
A-2	1	5 VIII 66	0607	26-33	15	C	47	31	29	2.82	1.6-5.1
A-3	1	5 VIII 66	0701	33-35	15	D	73	41	34	4.02	2.2-6.2
A-3	2	5 VIII 66	0701	33-35	24	D	18	20	20	5.78	2.2-8.6
A-4	1	5 VIII 66	0840	49-55	15	D	119	217	193	3.14	1.6-5.7
A-4	2	5 VIII 66	0840	49-55	33	D	4	54	49	5.11	2.4-6.9
A-5	1	5 VIII 66	1219	58-57	15	D	6	144	141	5.03	2.7-8.1
A-5	2	5 VIII 66	1219	58-57	33	D	8	120	116	5.26	2.1-8.6
A-6	1	5 VIII 66	1441	68-71	15	D	71	144	131	4.00	2.2-6.6
A-6	2	5 VIII 66	1441	68-71	33	D	—	424	401	5.79	2.0-9.2
A-7	1	5 VIII 66	1741	102-113	15	D	5	7	5	3.58	2.3-4.3
A-7	2	5 VIII 66	1741	102-113	33	D	10	40	36	4.18	2.2-10.1
B-1	1	6 VIII 66	1349	24-16	15	D	—	2	1	2.60	2.6
B-2	1	6 VIII 66	1149	38-29	15	D	9	7	7	3.83	2.5-4.7
B-2	2	6 VIII 66	1149	38-29	21	D	1	29	22	3.58	2.1-7.1
B-3	1	6 VIII 66	1101	46-42	15	D	22	2	2	2.05	1.9-2.2
B-3	2	6 VIII 66	1101	46-42	33	D	2	10	10	3.34	2.1-6.5
B-4	1	6 VIII 66	0720	60-58	15	D	4	29	25	3.90	1.7-6.4
B-4	2	6 VIII 66	0720	60-58	33	D	—	15	15	5.53	2.9-9.2
B-5	1	6 VIII 66	0544	73-73	15	C	12	112	88	4.07	2.0-5.7
B-5	2	6 VIII 66	0544	73-73	33	C	2	85	65	6.22	2.2-13.0
B-6	1	6 VIII 66	0133	87-82	15	N	1	98	96	5.37	2.6-15.1
B-6	2	6 VIII 66	0133	87-82	33	N	—	172	149	6.81	3.0-16.7
B-7	1	5 VIII 66	2340	91-99	15	N	—	163	162	6.58	3.2-15.3
B-7	2	5 VIII 66	2340	91-99	33	N	—	726	701	8.53	3.5-25.9
C-1	1	7 VIII 66	0043	18-20	6	N	—	2	2	2.10	1.8-2.4
C-2	1	7 VIII 66	0137	27-29	15	N	1	—	—	—	—
C-3	1	7 VIII 66	0239	31-33	15	N	—	9	9	3.19	2.6-5.5
C-4	1	7 VIII 66	0413	40-40	15	N	4	41	39	3.66	1.7-6.3
C-4	2	7 VIII 66	0413	40-40	33	N	—	1	1	4.70	4.7
C-5	1	7 VIII 66	0745	48-48	15	D	2	—	—	—	—
C-5	2	7 VIII 66	0745	48-48	33	D	—	3	3	3.50	2.8-4.8

APPENDIX TABLE 1.—Continued.

Cruise and station	Net	Date	Start time	Depth of water (m)	Maximum tow depth (m)	Light regime[1]	Total number of eggs	Larvae			
								Total number captured	Number measured	Notochord length	
										Mean (mm)	Range (mm)
D-66-10—Continued			EDST								
C-6	1	7 VIII 66	1005	55-55	15	D	19	1	1	3.20	3.2
C-7	2	7 VIII 66	1406	70-60	33	D	—	7	6	5.30	4.5-6.0
C-8	1	7 VIII 66	1630	108-210	15	D	—	1	1	4.90	4.9
C-8	2	7 VIII 66	1630	108-210	33	D	—	87	73	5.39	3.3-7.3
D-5	1	8 VIII 66	0615	40-33	15	D	6	4	4	3.75	2.4-7.1
D-5	2	8 VIII 66	0615	40-33	24	D	—	1	1	3.20	3.2
D-6	1	8 VIII 66	0422	48-54	15	N	—	7	6	5.77	4.5-6.5
D-7	1	8 VIII 66	0018	77-75	15	N	—	21	20	5.95	4.5-13.5
D-7	2	8 VIII 66	0018	77-75	33	N	—	6	6	12.25	6.4-17.6
D-8	1	7 VIII 66	2221	110-126	15	N	—	1	1	3.60	3.6
D-8	2	7 VIII 66	2221	110-126	33	N	—	64	61	10.21	6.0-19.9
E-6	1	9 VIII 66	1306	44-42	15	D	—	1	1	5.30	5.3
E-6	2	9 VIII 66	1306	44-42	33	D	—	3	3	5.97	5.8-6.2
E-7	1	9 VIII 66	1505	64-64	15	D	—	2	2	3.30	2.9-3.7
E-7	2	9 VIII 66	1505	64-64	33	D	—	5	5	5.54	4.2-7.2
F-6	1	9 VIII 66	2306	55-53	15	N	—	1	1	6.00	6.0
F-6	2	9 VIII 66	2306	55-53	33	N	—	2	2	7.05	6.9-7.2
F-7	1	9 VIII 66	2118	77-71	15	N	—	7	7	7.50	5.5-10.1
G-5	1	21 VIII 66	1355	51-48	15	D	—	1	1	3.60	3.6
H-5	1	22 VIII 66	0239	37-44	15	N	—	1	1	14.80	14.8
H-5	2	22 VIII 66	0239	37-44	24	N	—	1	1	14.50	14.5
H-7	2	21 VIII 66	2130	95-163	33	N	—	2	2	15.10	15.0-15.2
J-7	2	23 VIII 66	0717	86-119	33	C	—	1	1	5.70	5.7
D-66-11			EDST								
A-2	1	13 IX 66	1133	29-31	15	D	15	2	2	2.95	2.6-3.3
A-2	2	13 IX 66	1133	29-31	24	D	7	9	7	3.03	2.6-3.7
A-3	1	13 IX 66	1243	38-42	15	D	190	13	12	3.65	2.5-4.8
A-3	2	13 IX 66	1243	38-42	24	D	23	9	8	3.86	2.8-4.6
A-4	1	13 IX 66	1415	46-53	15	D	7	136	131	4.17	2.2-6.2
A-4	2	13 IX 66	1415	46-53	33	D	22	91	86	3.78	2.3-6.5
A-5	1	13 IX 66	1816	60-60	15	C	112	197	187	4.49	1.8-6.7
A-5	2	13 IX 66	1816	60-60	33	C	116	201	198	4.77	1.8-7.5
A-6	1	13 IX 66	2030	68-68	15	N	—	86	83	5.82	2.7-11.9
A-6	2	13 IX 66	2030	68-68	33	N	9	131	123	5.86	4.1-11.5
A-7	1	14 IX 66	0104	113-112	12	N	—	81	63	5.00	3.7-20.0
A-7	2	14 IX 66	0104	113-112	30	N	—	113	107	5.24	2.9-21.0
B-1	1	14 IX 66	2304	26-26	6	N	—	13	10	2.70	2.4-3.2
B-2	1	14 IX 66	0025	33-35	15	N	—	13	9	2.76	2.4-3.1
B-3	1	17 IX 66	0033	49-51	15	N	36	38	32	4.18	2.3-9.4
B-3	2	17 IX 66	0033	49-51	33	N	19	567	558	5.60	2.4-17.3
B-4	1	14 IX 66	1743	60-66	15	C	9	12	12	3.50	2.3-5.8
B-4	2	14 IX 66	1743	60-66	33	C	3	178	178	4.86	2.4-13.0
B-5	1	14 IX 66	1359	73-71	15	D	22	2	2	5.60	4.8-6.4
B-5	2	14 IX 66	1359	73-71	33	D	23	103	96	4.14	2.0-11.0
B-6	1	14 IX 66	1004	80-84	15	D	4	12	4	7.05	4.9-8.8
B-6	2	14 IX 66	1004	80-84	33	D	—	39	38	6.57	5.1-7.8
B-7	1	14 IX 66	0457	95-93	15	C	—	10	10	11.65	6.7-40.0
B-7	2	14 IX 66	0457	95-93	33	C	—	53	51	12.05	6.5-41.1
C-1	1	17 IX 66	0850	18-16	9	D	—	4	4	3.05	2.7-3.7
C-2	1	17 IX 66	0758	29-26	15	D	—	5	3	2.73	2.6-2.8
C-3	1	17 IX 66	0707	38-29	15	C	56	—	—	—	—
C-4	1	17 IX 66	1640	40-42	15	D	8	1	1	4.40	4.4
C-4	2	17 IX 66	1640	40-42	33	D	4	312	300	4.20	2.3-10.3
C-5	1	17 IX 66	1835	49-47	15	C	16	8	7	3.04	2.5-4.5
C-5	2	17 IX 66	1835	49-47	33	C	1	157	157	6.92	2.8-11.9
C-6	2	17 IX 66	2033	57-57	33	N	23	208	207	5.61	2.1-19.5
C-7	1	17 IX 66	2247	71-77	15	N	—	13	12	12.32	3.1-22.5
C-7	2	17 IX 66	2247	71-77	33	N	—	351	345	8.49	3.1-32.8
C-8	1	18 IX 66	0049	110-519	15	N	—	2	2	8.25	7.9-8.6
C-8	2	18 IX 66	0049	110-519	33	N	—	2	2	9.70	9.4-10.0
D-2	1	18 IX 66	1421	22-20	6	D	—	1	1	3.60	3.6
D-3	1	18 IX 66	1326	20-26	15	D	—	6	5	2.80	2.2-4.0
D-4	1	18 IX 66	1159	33-27	15	D	—	12	11	3.39	2.6-4.2
D-4	2	18 IX 66	1159	33-27	24	D	—	11	11	2.78	2.2-4.2
D-5	1	18 IX 66	1043	35-35	15	D	—	25	22	3.82	2.6-5.9
D-5	2	18 IX 66	1043	35-35	33	D	—	136	130	4.93	2.6-11.2
D-6	1	18 IX 66	0843	55-53	15	D	—	22	22	5.99	4.1-8.8
D-6	2	18 IX 66	0843	55-53	33	D	—	372	363	5.48	3.1-12.2
D-7	1	18 IX 66	0624	73-70	15	C	—	1	1	8.80	8.8
D-7	2	18 IX 66	0624	73-70	33	C	—	61	61	6.96	3.5-10.2
D-8	2	18 IX 66	0424	121-115	33	N	—	56	55	9.14	6.5-12.7

APPENDIX TABLE 1.—Continued.

Cruise and station	Net	Date	Start time	Depth of water (m)	Maximum tow depth (m)	Light regime[1]	Total number of eggs	Larvae			
								Total number captured	Number measured	Notochord length	
										Mean (mm)	Range (mm)
D-66-12			EDST								
A-1	1	15 X 66	0402	24-9	6	N	—	3	2	3.40	3.1-3.7
A-2	1	15 X 66	0309	31-29	15	N	—	16	15	4.21	3.2-5.8
A-2	2	15 X 66	0309	31-29	24	N	—	31	30	4.06	2.8-5.3
A-3	1	15 X 66	0209	42-37	15	N	—	8	8	4.72	2.8-6.7
A-3	2	15 X 66	0209	42-37	33	N	1	37	33	4.94	2.6-26.5
A-4	1	15 X 66	0715	48-51	15	C	31	105	102	3.47	2.3-6.9
A-4	2	15 X 66	0715	48-51	33	C	63	216	207	3.47	2.3-5.7
A-5	1	15 X 66	0843	58-60	15	D	12	6	6	3.07	2.7-3.7
A-5	2	15 X 66	0843	58-60	33	D	275	73	67	2.98	2.0-4.6
A-6	1	15 X 66	1032	68-71	15	D	1	8	8	5.51	3.1-11.5
A-6	2	15 X 66	1032	68-71	33	D	2	191	177	4.69	1.8-12.8
A-7	1	15 X 66	1226	108-115	15	D	—	2	2	9.90	3.0-16.8
A-7	2	15 X 66	1226	108-115	33	D	—	40	40	13.54	3.7-21.5
B-1	1	14 X 66	1930	7-18	6	N	2	—	—	—	—
B-2	1	14 X 66	2037	33-37	15	N	6	1	1	2.80	2.8
B-2	2	14 X 66	2037	33-37	24	N	14	4	4	5.47	3.2-6.8
B-3	1	14 X 66	2134	42-48	15	N	10	1	1	3.30	3.3
B-3	2	14 X 66	2134	42-48	33	N	19	19	19	4.39	2.2-8.8
B-4	1	14 X 66	1406	62-58	15	D	6	6	6	5.75	4.2-6.8
B-4	2	14 X 66	1406	62-58	33	D	9	145	142	6.36	2.5-18.5
B-5	1	14 X 66	1238	71-71	15	D	2	24	23	9.59	4.1-14.1
B-5	2	14 X 66	1238	71-71	33	D	1	204	200	7.51	2.7-13.8
B-6	1	14 X 66	0850	82-80	15	D	—	31	31	10.20	4.3-16.5
B-6	2	14 X 66	0850	82-80	33	D	—	276	276	10.81	2.2-21.0
B-7	1	14 X 66	0710	91-90	15	C	—	15	15	11.16	6.3-15.7
B-7	2	14 X 66	0710	91-90	33	C	—	59	58	9.63	3.5-15.0
C-2	1	13 X 66	1012	22-27	15	D	—	3	3	8.73	4.2-15.2
C-3	1	13 X 66	1105	31-31	15	D	1	5	5	7.14	3.5-13.2
C-3	2	13 X 66	1105	31-31	24	D	2	15	15	5.65	4.4-7.2
C-4	1	13 X 66	1233	37-40	15	D	—	38	38	5.77	2.6-9.2
C-4	2	13 X 66	1233	37-40	33	D	2	65	62	6.74	2.6-13.0
C-5	1	13 X 66	1555	48-46	15	D	11	34	33	4.98	2.6-7.3
C-5	2	13 X 66	1555	48-46	33	D	7	161	161	5.99	2.6-11.7
C-6	1	13 X 66	1814	55-55	15	C	1	34	34	7.64	3.1-12.2
C-6	2	13 X 66	1814	55-55	33	C	17	100	99	7.84	2.2-16.3
C-7	1	13 X 66	2147	77-70	15	N	4	45	43	13.54	3.9-29.2
C-7	2	13 X 66	2147	77-70	33	N	3	490	487	9.90	2.3-33.8
C-8	1	13 X 66	2359	198-787	15	N	—	1	1	19.80	19.8
C-8	2	13 X 66	2359	198-787	33	N	—	1	1	12.80	12.8
D-1	1	6 X 66	0224	16-20	6	N	—	1	1	2.70	2.7
D-3	1	6 X 66	0408	26-22	15	N	—	3	3	7.13	6.9-7.4
D-4	2	13 X 66	0036	31-22	24	N	2	1	1	15.00	15.0
D-5	1	12 X 66	2304	35-37	15	N	1	1	1	6.20	6.2
D-5	2	12 X 66	2304	35-37	24	N	30	4	4	6.07	4.6-8.3
D-6	1	12 X 66	1901	55-53	15	C	8	125	121	6.18	2.5-18.3
D-6	2	12 X 66	1901	55-53	33	C	3	134	130	6.94	1.6-17.7
D-7	1	12 X 66	1702	70-75	15	C	5	46	45	4.18	3.0-6.7
D-7	2	12 X 66	1702	70-75	33	C	7	42	42	5.58	3.4-8.3
D-8	1	12 X 66	1313	99-121	15	D	36	1	1	2.90	2.9
D-8	2	12 X 66	1313	99-121	33	D	9	39	35	4.50	2.8-6.7
E-4	1	11 X 66	2134	29-29	15	N	33	1	1	2.80	2.8
E-5	1	11 X 66	2310	35-35	15	N	1	21	21	6.37	2.9-20.2
E-5	2	11 X 66	2310	35-35	24	N	1	15	15	5.10	2.7-7.6
E-6	1	12 X 66	0250	44-42	15	N	3	35	34	6.64	3.1-25.0
E-6	2	12 X 66	0250	44-42	33	N	—	18	18	8.49	4.5-23.4
E-7	1	12 X 66	0452	64-66	15	N	1	7	7	7.99	4.7-14.1
E-7	2	12 X 66	0452	64-66	33	N	—	52	52	10.04	2.8-31.4
E-8	1	12 X 66	0903	157-121	15	D	—	4	4	3.52	2.8-4.4
E-8	2	12 X 66	0903	157-121	33	D	—	2	2	3.00	2.8-3.2
F-5	1	4 X 66	2251	37-33	15	N	—	2	2	5.60	4.2-7.0
F-5	2	4 X 66	2251	37-33	24	N	1	1	1	3.70	3.7
F-6	1	4 X 66	2053	53-55	15	N	—	63	62	6.54	2.9-23.3
F-6	2	4 X 66	2053	53-55	33	N	—	10	9	7.03	3.7-13.8
F-7	1	4 X 66	1652	104-79	15	D	—	6	6	4.68	3.0-7.0
F-7	2	4 X 66	1652	104-79	33	D	—	21	17	6.33	3.0-9.3
G-4	1	4 X 66	0727	29-33	15	C	—	1	1	5.40	5.4
G-5	2	4 X 66	0916	49-53	33	D	—	2	2	4.65	3.5-5.8
G-6	2	4 X 66	1309	95-75	33	D	1	1	1	7.40	7.4
H-6	1	3 X 66	0711	88-66	15	C	2	—	—	—	—
H-6	2	3 X 66	0711	88-66	33	C	—	1	1	15.00	15.0
J-7	2	3 X 66	0055	79-91	33	N	—	1	1	22.50	22.5
K-7	1	30 IX 66	1950	823-914	15	N	—	1	1	11.00	11.0

APPENDIX TABLE 1.—Continued.

Cruise and station	Net	Date	Start time	Depth of water (m)	Maximum tow depth (m)	Light regime[1]	Total number of eggs	Larvae			
								Total number captured	Number measured	Notochord length	
										Mean (mm)	Range (mm)
D-66-14			EST								
A-1	1	4 XII 66	1956	26-9	3	N	—	2	1	6.50	6.5
A-2	1	4 XII 66	1857	33-29	15	N	—	2	2	5.60	5.4-5.8
A-3	1	4 XII 66	1750	44-33	15	N	—	2	2	5.95	5.9-6.0
A-3	2	4 XII 66	1750	44-33	24	N	—	1	1	3.10	3.1
A-4	1	4 XII 66	1618	53-51	15	C	—	5	5	5.44	4.9-5.7
A-4	2	4 XII 66	1618	53-51	33	C	—	6	6	5.00	4.2-6.4
A-5	2	4 XII 66	1449	58-58	33	D	—	3	3	4.93	4.1-5.5
A-6	1	4 XII 66	1255	73-68	15	D	—	3	3	6.30	6.0-6.6
A-6	2	4 XII 66	1255	73-68	33	D	—	2	2	3.60	2.8-4.4
B-1	1	3 XII 66	1937	18-22	6	N	—	1	1	6.10	6.1
B-2	1	3 XII 66	2056	31-42	15	N	—	1	1	3.60	3.6
B-2	2	3 XII 66	2056	31-42	24	N	—	2	2	5.60	3.0-8.2
B-3	1	3 XII 66	2210	44-51	15	N	—	19	18	5.55	3.2-7.2
B-3	2	3 XII 66	2210	44-51	33	N	—	25	25	5.93	4.2-7.6
B-4	1	3 XII 66	2351	62-71	15	N	—	4	4	4.10	2.9-6.5
B-4	2	3 XII 66	2351	62-71	33	N	—	5	5	8.70	4.5-23.2
B-5	1	4 XII 66	0113	73-73	15	N	—	2	2	8.80	5.7-11.9
B-6	1	4 XII 66	0310	84-84	15	N	—	1	1	8.50	8.5
B-6	2	4 XII 66	0310	84-84	33	N	—	1	1	6.50	6.5
C-3	2	3 XII 66	1047	33-37	24	D	—	1	1	5.10	5.1
C-4	1	3 XII 66	0412	42-40	15	N	—	5	5	15.56	4.1-56.9
C-4	2	3 XII 66	0412	42-40	33	N	—	8	8	4.99	3.6-7.4
C-5	1	2 XII 66	2302	49-47	15	N	—	25	25	5.67	3.5-7.4
C-5	2	2 XII 66	2302	49-47	33	N	—	22	22	5.74	3.5-8.4
C-6	1	2 XII 66	2022	57-57	15	N	—	19	19	7.29	3.1-33.9
C-6	2	2 XII 66	2022	57-57	33	N	—	21	21	5.06	3.1-7.7
C-7	1	2 XII 66	1727	77-70	15	N	—	17	15	7.13	3.2-12.8
C-7	2	2 XII 66	1727	77-70	33	N	—	7	7	11.56	4.4-43.1
D-6	1	2 XII 66	0652	51-53	15	C	—	18	17	4.78	3.1-6.9
D-6	2	2 XII 66	0652	51-53	33	C	—	18	17	5.07	2.7-6.5
D-7	1	2 XII 66	0920	73-79	15	D	—	1	1	6.20	6.2
D-7	2	2 XII 66	0920	73-79	33	D	—	1	1	6.10	6.1
E-6	1	10 XI 66	0722	42-40	15	C	1	1	1	3.60	3.6
E-6	2	10 XI 66	0722	42-40	33	C	—	4	4	3.82	3.5-4.2
E-7	1	10 XI 66	1200	68-62	15	D	—	1	1	29.60	29.6
E-7	2	10 XI 66	1200	68-62	33	D	—	2	2	5.05	4.0-6.1
E-8	1	19 XI 66	0201	110-95	15	N	8	1	1	23.80	23.8
E-8	2	19 XI 66	0201	110-95	33	N	—	1	1	6.00	6.0
F-5	1	11 XI 66	0126	37-38	15	N	—	1	1	3.80	3.8
F-6	1	10 XI 66	2303	51-51	15	N	—	4	4	15.90	8.5-24.2
F-6	2	10 XI 66	2303	51-51	33	N	—	4	4	8.22	6.0-12.9
F-7	1	18 XI 66	2203	68-70	15	N	—	36	36	29.49	20.4-36.5
F-7	2	18 XI 66	2203	68-70	33	N	—	61	61	28.63	16.7-39.3
G-5	1	11 XI 66	2234	51-46	15	N	1	4	4	12.75	3.8-22.6
G-5	2	11 XI 66	2234	51-46	33	N	—	1	1	7.30	7.3
G-6	1	12 XI 66	0050	79-97	15	N	8	6	6	15.17	5.7-24.6
G-6	2	12 XI 66	0050	79-97	33	N	2	9	9	6.99	2.5-17.9
H-5	1	12 XI 66	0754	40-44	15	D	—	2	2	6.80	6.6-7.0
H-5	2	12 XI 66	0754	40-44	33	D	—	1	1	7.10	7.1
H-6	1	12 XI 66	0609	84-82	15	C	1	—	—	—	—
H-6	2	12 XI 66	0609	84-82	33	C	3	3	3	4.73	3.9-5.2
H-7	1	12 XI 66	0503	97-172	15	N	5	—	—	—	—
H-7	2	12 XI 66	0503	97-172	33	N	5	4	4	5.60	2.4-10.4
J-5	1	14 XI 66	1727	26-27	15	C	—	1	1	6.70	6.7
J-6	1	14 XI 66	1935	35-35	15	N	—	1	1	7.60	7.6
J-6	2	14 XI 66	1935	35-35	24	N	—	2	2	8.20	7.6-8.8
J-7	2	14 XI 66	2329	90-71	33	N	—	3	3	4.83	3.2-6.3
K-1	1	18 XI 66	0842	13-16	6	D	—	1	1	3.10	3.1
K-6	1	17 XI 66	2236	53-40	15	N	13	—	—	—	—
K-6	2	17 XI 66	2236	53-40	33	N	4	—	—	—	—
K-7	2	17 XI 66	2127	483-311	33	N	2	—	—	—	—
L-5	2	17 XI 66	1545	88-622	33	C	1	1	1	4.30	4.3
M-4	1	16 XI 66	2339	58-24	6	N	—	1	1	2.90	2.9

[1]Light regime: D = day tow; N = night tow; C = crepuscular tow (when any part of a tow occurred within 1 h of sunrise or sunset).

DISTRIBUTION, VARIATION, AND SUPPLEMENTAL DESCRIPTION OF THE OPOSSUM SHRIMP, *NEOMYSIS AMERICANA* (CRUSTACEA: MYSIDACEA)

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ABSTRACT

Neomysis americana ranges from the Gulf of St. Lawrence to northeastern Florida in estuaries and nearshore ocean and to depths of 100 m on Georges Bank. Samples studied from localities between Nova Scotia and Georgia show no consistent geographic variation. Specific characters are illustrated and discussed.

Neomysis americana (S. I. Smith, 1873) is the most common mysid in shallow marine waters of eastern North America. In his monograph, W. M. Tattersall (1951) gave the range as "from the Gulf of St. Lawrence to the coast of Virginia in shallow water." Since then its known distribution has been extended south to North Carolina (Wigley and Burns, 1971) and recently to South Carolina and Georgia (Sikora, Heard, and Dahlberg, 1972; Williams, 1972). Further details of its distribution are given below.

Published and unpublished distributional data available to us before the present study was undertaken suggested the possible existence of two isolated populations of *Neomysis*: 1) a population north of Cape Henry, Va., mostly in coastal waters but also occurring in large numbers on Georges Bank; 2) a population confined mainly to sounds and estuaries from North Carolina to Georgia. We suspected that there might be taxonomic differences between these or other populations, a likelihood that had occurred independently to other investigators (Bousfield, in litt.; Heard, in litt.). *Neomysis americana* develops two or more generations per year, at least in the United States (Hopkins, 1965), small summer animals and large winter animals. The latter from North Carolina estuaries showed apparent differences that we felt merited further investigation. We decided to determine variation and geographic distribution more precisely in *N. americana*.

The study is a complement to current ecological investigations in coastal environments. *Neomysis americana* is probably an omnivore like its near relative *N. integer* (Mauchline, 1971) or *Mysis relicta* (Lasenby and Langford, 1973), consuming organic detritus, smaller crustaceans, and diatoms and fitting the trophic role attributed to other mysids preyed upon by fishes in Florida estuaries (Odum and Heald, 1972) and Japan (Ii, 1964). It is known to be a significant element in the diet of fishes such as flounder, shad, mackerel, and anchovy (Hopkins, 1965), *Paralichthys dentatus* and *P. lethostigma* (Powell, in litt.), and the hakes, *Urophycis regius* and *U. floridanus* (Sikora et al., 1972) as well as other fishes (Taylor, in litt.).

MATERIALS AND METHODS

Our materials for study were both reliable literature records and museum specimens. Canadian occurrences have been reported by Bousfield (1955, 1956a, b, 1958, 1962), O. S. Tattersall (1955a), Bousfield and Leim (1960), Préfontaine and Brunel (1962), and Brunel (1970). Records from the United States included those of Whiteley (1948), Hulbert (1957), Herman (1963), and Wigley and Burns (1971) in addition to others cited previously. Southern range limits and offshore distribution were partly established by examination of plankton samples taken in waters between Cape Hatteras, N.C., and Jupiter Inlet, Fla., during cruises 4, 5, 7, 8, 9 of MV *Theodore N. Gill* (October 1953-December 1954), concentrating on nearshore samples where the species was expected to occur (station data in Anderson, Moore, and Gordy, 1961a, b). Specimens studied

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for variation were from collections in the National Museum of Natural History (USNM), including new collections acknowledged below.

Measurements and counts used in assessing variation were: 1) carapace length from rear edge of orbit to posterolateral margin, 2) length and width of antennal scale (ventral view), 3) lengths of inner and outer uropods, 4) number of spines in ventral comblike row on inner uropod near distomesial margin of statocyst vesicle, 5) length of this row of spines, 6) number of spines per 0.01 mm in this row, 7) number of spines on margin of telson, and 8) relative widths of cornea and eyestalk. External morphology of representative specimens from over the range was studied and compared.

Specimens measured for comparisons were mature adults (mainly females) from the following collections: USNM 89736, St. Andrews, near Atlantic Biological Station, N.B.; USNM 82658 and 82651, Woods Hole, Mass., received 2 January 1907, Vinal N. Edwards, collector; USNM 78734, Amityville, Long Island, N.Y., 6 August 1938, H. K. Townes, collector; USNM 143770, York River below West Point, Va., 14 January, 1964, W. A. Van Engel, collector; USNM 143771, Garbacon Shoal, 6 May 1964, W. C. Noe, collector, and USNM 143772, Wilkinson Point, 17 June 1964, Frank Holland, collector, Neuse River, N.C.; USNM 143773, Wassau Sound, Ga., 29 August 1972, and USNM 143774, mouth of St. Catherines Sound, Ga., 30 January 1970, Richard W. Heard, Jr., collector. All specimens were large winter animals except the samples of summer animals from Amityville, N.Y., and Wassau Sound, Ga.

RESULTS AND DISCUSSION

Morphological Analysis

Proportional and meristic characters were evaluated for variation in different parts of the range. Mean carapace length in millimeters (rear edge of orbit to posterolateral margin) for the samples analyzed were: (Figure 1) New York, 2.95; (Figures 1, 2) New Brunswick, 3.03; Massachusetts, 3.25; Virginia, 3.51; North Carolina, 3.03; Georgia, St. Catherines Sound, 3.91 - Wassau Sound, 2.09; (Figure 3) New Brunswick, 3.01; North Carolina, 2.74; Georgia, as above. There is no detectable difference in size between males and females of assumed comparable age.

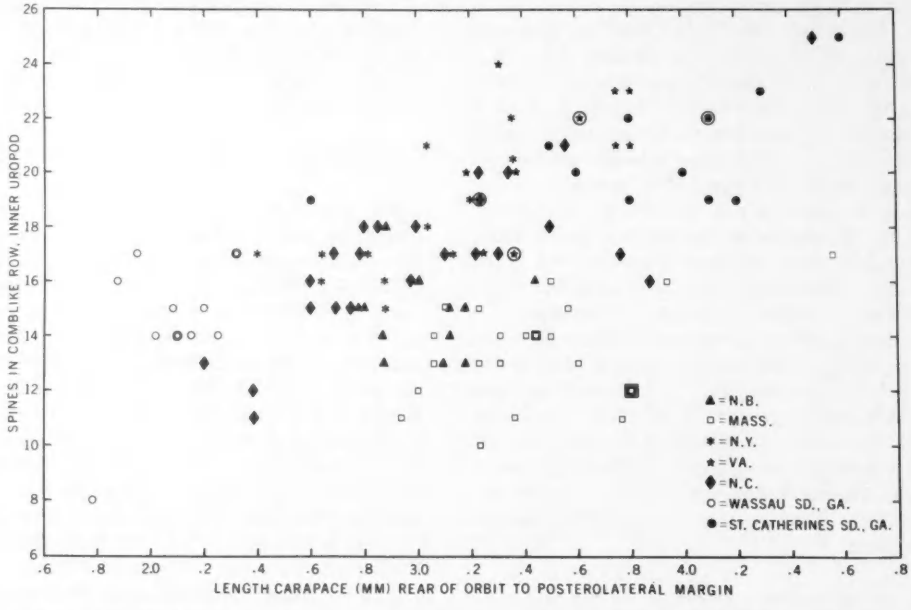
SPINES IN COMBLIKE ROW, INNER UROPOD
LENGTH CARAPACE (MM) REAR OF ORBIT TO POSTEROLATERAL MARGIN
▲ = N.B.
□ = MASS.
✱ = N.Y.
★ = VA.
◆ = N.C.
○ = WASSAU SD., GA.
● = ST. CATHERINES SD., GA.

FIGURE 1.—Relation between number of spines in comblike row on inner uropod and length of carapace from rear edge of orbit to posterolateral margin in seven populations of *Neomysis americana*. Framed points = replicates.

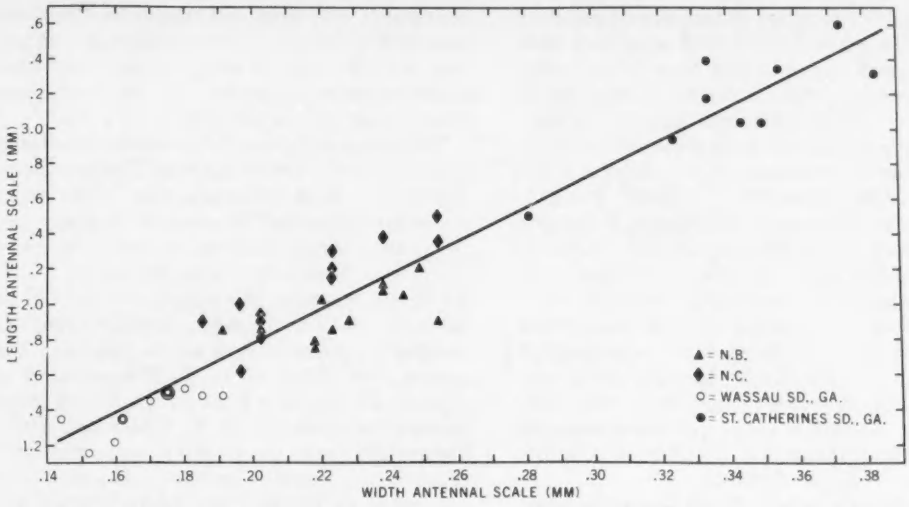

FIGURE 2.—Relation between length and width of antennal scale in four populations of *Neomysis americana*. Framed points = replicates

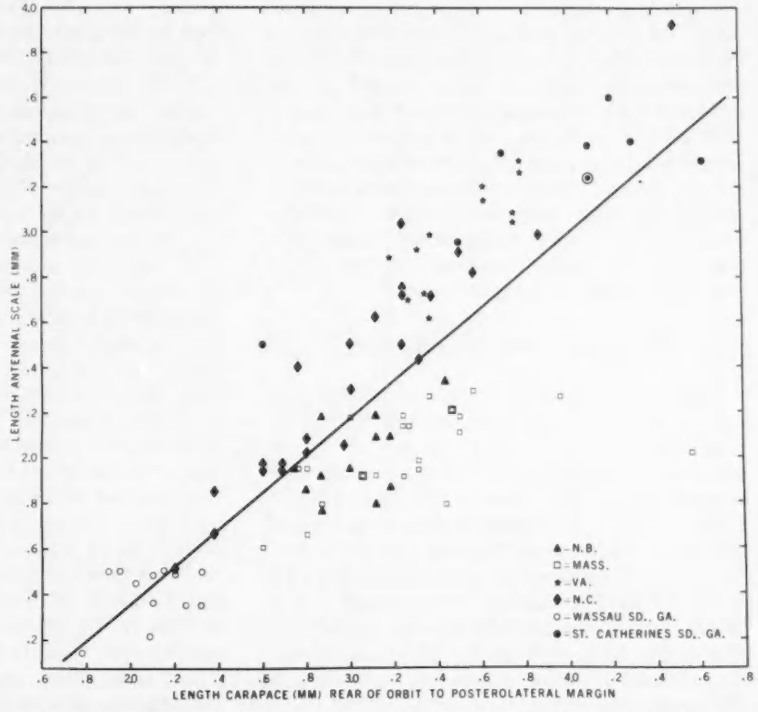
LENGTH ANTENNAL SCALE (MM)
LENGTH CARAPACE (MM) REAR OF ORBIT TO POSTEROLATERAL MARGIN
▲ - N.B.
□ - MASS.
▪ - VA.
♦ - N.C.
○ - WASSAU SD., GA.
● - ST. CATHERINES SD., GA.

FIGURE 3.—Relation between length of antennal scale and length of carapace from rear edge of orbit to posterolateral margin in six populations of *Neomysis americana*. Framed points = replicates.

The number of spines in the ventral comblike row on the inner uropod first suggested that northern populations might have fewer spines than those in the south. This proves not to be true; rather, the number of spines is apparently a function of body size (Figure 1). A regression analysis shows that the relationship is nonlinear ($Y = 3.39X + 6.08$, $r = 0.579$, $z = 0.661$, $P>0.05$), falling short of statistical significance. Inspection of the scatter of points indicates that number of spines more or less levels off at upper size limits, but distribution is fairly broad at all sizes.

Two other relationships do yield statistically significant correlations but show no geographic association. Length of the antennal scale is correlated with its width (Figure 2) ($Y = 9.726X - 0.177$, $r = 0.967$, $z = 2.043$, $P<0.05$) and with carapace length (Figure 3) ($Y = 0.813X - 0.264$, $r = 0.822$, $z = 1.162$, $P<0.05$).

Other plots analyzed but not discussed in detail here show similar relationships which further substantiate the facts given above: length of comblike row of spines on inner uropod plotted against length of carapace; length of comblike row of spines on inner uropod plotted against longest spine in row; length of inner uropod plotted against length of carapace; number of spines per 0.01 mm in comblike row of spines on inner uropod plotted against length of carapace. Size of cornea, shape of rostrum, shape of antennal scale, spination of telson, and relative lengths of uropods on specimens from throughout the range were compared. No constant differences were noted that would define geographic races.

Supplemental Description

Despite its abundance, *Neomysis americana* has not been described and illustrated fully. The reason for this omission is obvious: of the 16 known species of *Neomysis*, it is the only one that occurs in the western North Atlantic and is not likely to be confused with any other mysid within its range. Three mysid genera are similar to *Neomysis: Acanthomysis, Paracanthomysis*, and *Proneomysis*. The last two are confined to the North Pacific, and the only Atlantic representative of the 13 known species of *Acanthomysis, A. longicornis* (Milne Edwards), is limited to European waters.

However, the lack of an adequate description of *N. americana* gave Ii (1964) some difficulty before he decided not to identify a *Neomysis* from Korea as *N. americana* but to describe it as a new species, *N. orientalis*. To obviate problems such as this, we offer Figures 4A-K and 5A-J and comments on some characters for which adequate illustrations are not available.

The rostrum (Figure 4A) is broadly rounded as in *N. intermedia* and *N. japonica*. The eyes are as described by W. M. Tattersall (1951), with a broad cornea occupying half the eyestalk. Medially, just before the eyestalk narrows, it is produced into a low protuberance armed with short setae. W. M. Tattersall described the telson (Figure 4K) as having about 40 spines on each lateral margin; the number of spines depends on the body size and ranges from about 20 to 40. The peduncle of antenna 1 is shown in Figure 4B, C, D, the latter showing the male lobe. W. M. Tattersall's (1951) Figure 77A shows the antennal scale without a suture, which would be unique for the genus. Our specimens have a distinct suture (Figure 4D) setting off a short distal segment. As in other species of *Neomysis* the labrum is produced anteriorly into a spiniform process (Figure 4E, F), and the terminal segment of the mandibular palp (Figure 4G) is relatively slender.

According to W. M. Tattersall (1951) the "tarsus" of pereopods 2-7 is 8-9 segmented. We find that the number of segments increases with body size (Figure 5A, C) as in *N. patagona* (O. S. Tattersall, 1955b; Holmquist, 1957). The proximal suture may be incomplete, not present medially; in such pereopods an additional tarsal segment would be counted when viewed laterally. Our counts are in lateral view and include both partly fused proximal segments. Small juveniles have 6 segments; small adults from Pamlico Sound, N.C., 7 segments; large adults from Woods Hole, Mass., 8 segments; and large adults from the York River, Va., 9 segments. The number appears to be rather constant among the pereopods of an individual, but may differ by 1 segment in one or two of the pereopods.

The genus *Neomysis* is unique in having median fingerlike papillae on the last two or three pereonal sterna of gravid females (W. M. Tattersall, 1932). W. M. Tattersall (1951) found these papillae on the last two sternae of *N. americana*, and we show them in Figure 4J. Their function is unknown. Other characters of *Neomysis* are the presence of a bailing lobe on the posterior margin of the oostegite of pereopod 6 (Figure 5E) and a rudimentary oostegite on pereopod 5 (Figure 5D).

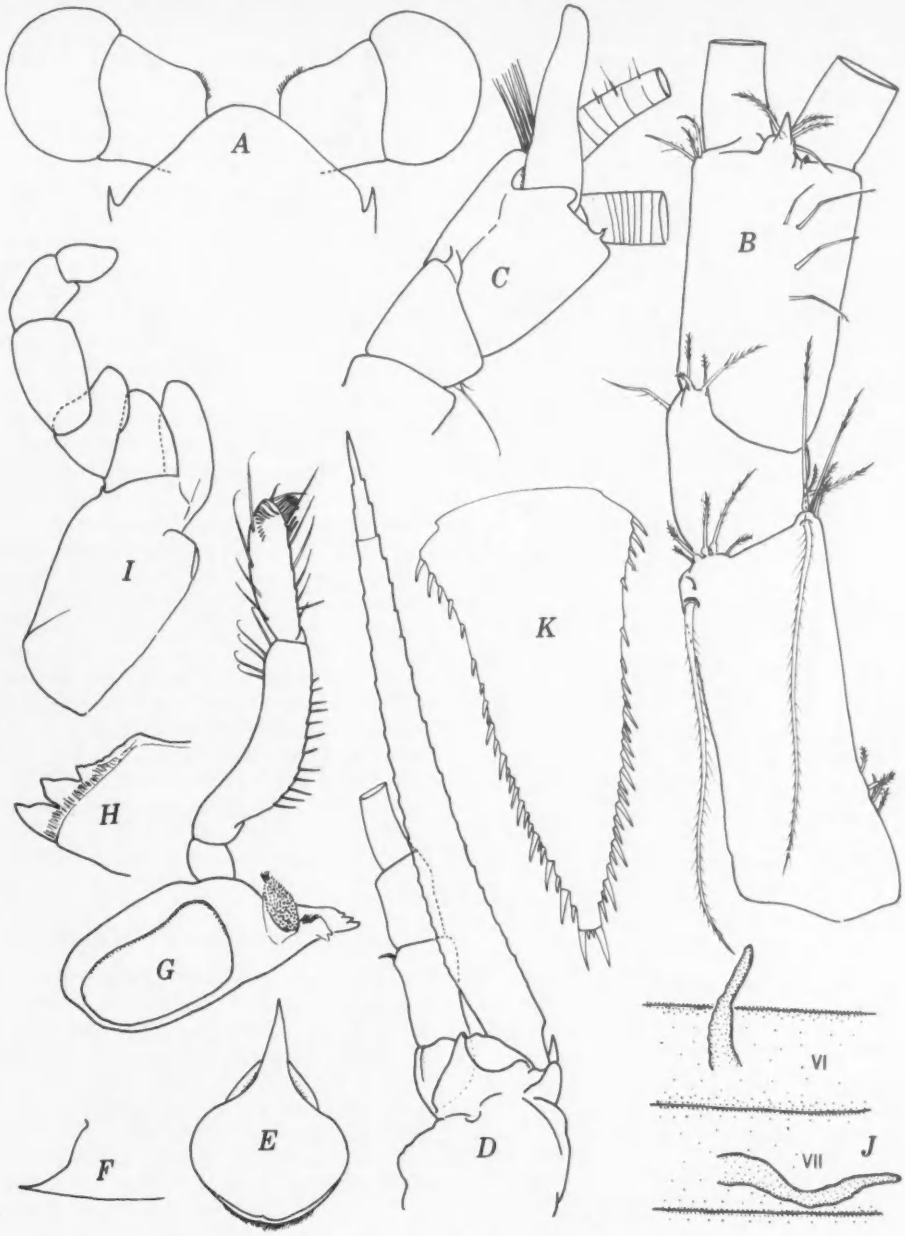

FIGURE 4.—*Neomysis americana*. A, Rostrum and eyes, dorsal (♀, New Brunswick). B, Right antenna 1 peduncle, dorsal, (♀, New Brunswick). C, Antenna 1 peduncle, ventral, (♂, York River, Va.). D, Antenna 2, ventral (♂, Adams Creek, N.C.). E, Labrum, ventral (♀, Pamlico Sound, N.C.). F, Same, lateral. G, Left mandible (♀, New Brunswick). H, Incisor of same. I, Right maxilliped, posterior, setae omitted (♂, York River). J, Sternal processes of pereonites VI and VII. K, Telson, dorsal (♂, Adams Creek).

FIGURE 5.—*Neomysis americana*. A, Endopod of pereopod 6 (♀, New Brunswick). B, Apex of same. C, Endopod of pereopod 7 (♀, New Brunswick). D, Oostegite of pereopod 5. E, Oostegite of pereopod 6 (arrow points to bailing lobe). F, Pleopod 4, ♂. G, Apex of same. H, Uropod, ventral (♀, Pamlico Sound, N.C.). I, Spine row of inner uropod (♂, Nova Scotia). J, Same, (♂, Adams Creek, N.C.).

Distribution

Neomysis americana inhabits estuaries and nearshore ocean from mesohaline reaches of the St. Lawrence River near St. Joachim on the north shore and Montmagny on the south, downstream around the Gaspé Peninsula, and from southern Newfoundland southward through the maritime provinces of Canada, along the United States to St. Augustine, Fla. Collections south of St. Augustine yielded no specimens, but the species may range as far southward as Cape Canaveral.

Prominent in estuaries, *N. americana* is also found at sea. Whiteley (1948) recorded it on Georges Bank inside the 100-m margin but most abundantly in water 75 m deep or less. Wigley and Burns (1971) showed essentially this pattern in their distribution summary. It was partly the distribution shown by these samples produced with the aid of grab samplers and dredges at a great number of stations to depths beyond 100 m between Nova Scotia and southern Florida that suggested an oceanic population north of Cape Henry, Va., separated from a southern estuarine one. None of their southern samples contained *N. americana*.

Neomysis americana was found in only four samples (total of 10 specimens) from the *Theodore N. Gill* material. These were: Cruise 4, 5 October-4 November 1953, Station 56 off Myrtle Beach, S.C. (2) - Cruise 9, 3 November-12 December 1954, Station 22 off St. Augustine, Fla. (1); Station 23 off mouth of St. Johns River, Fla. (6); Station 56 (1). All these stations were in water 10 m deep or less.

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NOTES

THE MEAN ANNUAL CYCLE OF COASTAL UPWELLING OFF WESTERN NORTH AMERICA AS OBSERVED FROM SURFACE MEASUREMENTS

One of the world's major upwelling regions lies off the west coast of the United States and northern Mexico. This paper summarizes marine surface observations to describe the normal yearly cycle of intensity of upwelling for the major portion of the northeastern Pacific coastal upwelling region.

Sverdrup (1938) applied Ekman's (1905) theory to account for a coastal upwelling situation observed off southern California. He proposed a mechanism by which water is transported offshore in the surface Ekman layer due to the stress of the wind on the sea surface and is replaced by water upwelled from depth. Wooster and Reid (1963) presented evidence that this is, indeed, the dominant mechanism acting in regions of slow, diffuse eastern boundary currents wherein lie the major coastal upwelling areas of the world, including that of the northeastern Pacific.

Our approach is to define the mean annual cycle of offshore Ekman transport along the west coast of the United States and the immediately adjacent regions of Canada and Mexico and to correlate this with features indicative of upwelling which appear in the long-term mean monthly distributions of sea surface temperature.

Marine surface weather observations for this study were obtained from a version of the National Climatic Center's tape deck of marine surface observations (Tape Data Family-11) in use at the U.S. Navy Fleet Numerical Weather Central. The observations in this file come primarily from merchant and naval ships and sometimes contain various errors in position, measurement, or processing. Consequently, the sea surface temperature data were subjected to an editing process which consisted of two filters. First, a gross error check was performed to eliminate nontemperatures. Second, the data were checked by comparison with a running mean of 10 reports. When a report of sea surface temperature differed from the running mean by greater than 9°C, the report was rejected. Wind speeds of greater than 100 m/s were rejected. "Variable" winds (no direction reported, low reported speed) were treated as calms.

The Ekman transport was calculated by the following procedure. The stress vector was computed from each wind observation according to the classical square law:

$$\vec{\tau} = \rho_a C_D |\vec{v}| \vec{v},$$

where $\vec{\tau}$ is the stress of the wind on the sea surface, ρ_a is the density of air (0.00122 g/cm^3), C_D is an empirical drag coefficient (0.0013), $\vec{v}$ is the observed wind velocity vector, and $|\vec{v}|$ is the observed wind speed. The resultant Ekman wind stress transport, $\vec{M}$, was computed according to,

$$\vec{M} = \frac{1}{f} \vec{\tau} \times \vec{k}$$

where $\vec{\tau}$ is the wind stress vector, f is the Coriolis parameter, and $\vec{k}$ is a unit vector directed vertically upward.

Figure 1 displays composite monthly values of these data for the 20-yr period, 1948-67. The plot on the left displays time series isograms of offshore component of Ekman transport while the central plot shows similar isograms of sea surface temperature. The coordinates are north-south distance on the ordinate and time by month on the abscissa. Each plot represents about 75,000 individual observations made within the 1° squares shown in the coastline plot to the right. The number of reports per 1° square per month was in the range 22 (in January off Vancouver Island) to 1,884 (in October off Los Angeles).

The sea surface temperature plot reveals a normal north-south gradation of temperature and a seasonal warming-cooling cycle with minima from February to April and maxima in August and September. The effects of upwelling are seen as distortions of this general pattern.[1]

In the northern portion, Cape Blanco to Vancouver Island, offshore Ekman transport is weak and occurs from about May through

[1]The fine scale details of the temperature distribution are masked by the 1° square spatial averages. For a detailed treatment of the mean temperature cycle in the southern portion of the region the reader is referred to Lynn (1967).

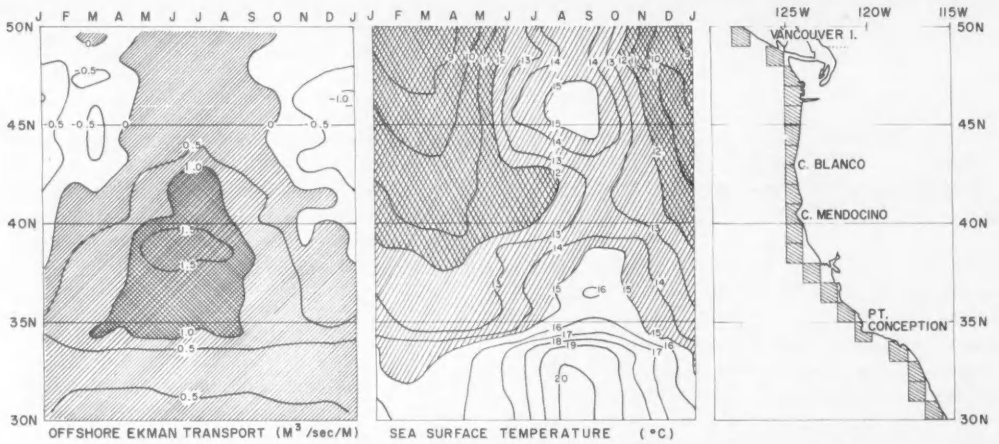

FIGURE 1.—Time series isograms of long-term composite monthly offshore Ekman transports (m^3/s per meter of coastline) and sea surface temperature (degrees Celsius) for the 20-yr (1948-67) period within the indicated 1° coastal squares.

September. The weakness of the transport is reflected by the presence of substantial seasonal warming. The region defined by temperatures greater than 15°C, located off Washington-Oregon during late summer, probably reflects the warming of the low-salinity Columbia River plume water which spreads over a large area of ocean surface. Some of the apparent warming may be due also to the concavity of the coastline in this area which could cause a greater proportion of the observations to be taken farther offshore, both because the 1° squares extend farther off the coast and because the coastwide shipping tracks may be displaced offshore.

South of Cape Blanco an abrupt increase of summer offshore Ekman transport is indicated, particularly during June and July. This is associated with a suppression of seasonal warming during early summer. Consequently, the period of maximum sea surface temperature is delayed until September when offshore transport has relaxed considerably.

South of Cape Mendocino Ekman transport is directed offshore for virtually the entire year and reaches its greatest value for the whole coast at about lat. 39°N during May through August. This maximum corresponds to an extreme suppression of seasonal warming indicated by nearly horizontal isotherms in the figure.

South of Point Conception, the offshore Ekman transport, although remaining generally positive throughout the year, is small and an abrupt southward increase in temperature, particularly during the summer, is apparent. Due to the tendency for a cyclonic eddy to form in the Southern California Bight (Reid, Roden, and Wyllie, 1958), warm advection not directly related to upwelling may be an important factor in this increase.

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THE RESIDUAL LIPIDS OF FISH PROTEIN CONCENTRATES

Previous papers (Medwadowski, Van der Veen, and Olcott, 1967, 1968; Medwadowski et al., 1971), presented data on the residual lipids in fish protein concentrates (FPCs) from red hake, *Urophycis chuss*; Gulf menhaden, *Brevoortia patronus*; pout, *Macrozoarces americanus*; and alewife, *Alosa pseudoharengus*; and some preliminary data on the effects of storage on the lipids. After 6 mo at 37° or 50°C, there were decreases in the contents of highly unsaturated fatty acids (C20:5 for alewife and C20:5 and C22:6 for pout and Gulf menhaden), and an appreciable decrease in the amount of lipid extractable from a menhaden FPC that originally contained 0.56% lipid, but no change in the amount extractable from FPCs that originally contained 0.11% (pout) or 0.06% (alewife) lipids.

In this paper we present data on the composition of lipids extracted from additional samples of FPCs (from Pacific hake, *Merluccius productus*; northern anchovy, *Engraulis mordax*; Atlantic menhaden, *Brevoortia tyrannus*; and Atlantic herring, *Clupea harengus harengus*) and also on the effects of storage, at several temperatures and humidities, on the composition of the residual lipids in a hake FPC preparation.

Materials and Methods

The FPCs had been prepared at National Marine Fisheries Service laboratories by countercurrent extraction of ground fish with hot isopropyl alcohol, followed by solvent removal and milling (Knobl et al., 1971).

Samples of a hake FPC were stored at the College Park Fishery Products Technology Laboratory at 21.1°, 32.3°, and 43.3°C and at 50% and 90% relative humidities for each temperature for periods of 1, 3, 6, and 12 mo (Green, 1972). The control was held at −29°C and ambient freezer humidity. The samples were shipped in plastic bags, cooled with dry ice (except for the zero time control sample which was shipped at ambient temperature), and stored at −18°C pending analyses.

Two procedures for determining moisture content (volatile matter) of the hake FPC samples were compared: 30-45 h at 110°-115°C, and 1 h at 130°C (Association of Official Analytical Chemists method, Horwitz, 1970:211). In the latter case, the drying was interrupted after 30 min; the caked meal was broken with a stirring rod; and the meal adhering to the rod was brushed back into the glass-stoppered weighing bottle in which the sample was being dried and weighed. Results from the two methods were in close agreement. The shorter method with the modification of the intermittent stirring was used thereafter.

The lipids were extracted (Soxhlet) in duplicate or triplicate with chloroform-methanol (2:1) from 200-g portions of the FPCs in large prewashed thimbles and analyzed as described by Medwadowski et al. (1971) with the following modifications in some cases. Purification was accomplished with a 2 × 22 cm Sephadex[1] column chromatography (Siakotas and Rouser, 1965; Rouser, Kritchevsky, and Yamamoto, 1967) and flow was by gravity. The saponification-methylation procedure used for determination of fatty acids was that described by Metcalfe, Schmitz, and Pelka (1966). The amounts of lipid were determined by drying aliquots of their solutions on a warm hot plate in preweighed disposable aluminum pans (Rouser et al., 1967).

Results and Discussion

Yields and fatty acid composition of the lipids extracted from seven separate runs—three from Pacific hake, two from northern anchovy, and one each from Atlantic herring and Atlantic menhaden—are shown in Table 1.

The two anchovy FPCs had somewhat similar fatty acid compositions; the main differences were in the amounts of C16:0 and C20:5. Herring FPC contained relatively larger percentages of C20:1 and C22:1. The Pacific hake FPCs, samples 8, 9, and 10, were similar in fatty acid composition but contained relatively more C18:1 than the FPCs from the other fish. The lipids of samples 8, 9, and 10, in general, resembled those of a red hake FPC, P-5 (reported previously by Medwadowski et al., 1967), and those of fresh red hake (Medwadowski et al., 1967, 1968). The Pacific hake FPCs, samples 8, 9, 10, and 78-103 (Table 3), contained higher percentages of C20:5 and C22:6 than red hake FPC P-5 and fresh red hake. Possibly less oxidation had occurred during processing, or the fish from which the FPCs were made had been subsisting on different foodstuffs.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—A comparison of lipids extracted from several fish protein concentrates.

FPC	Volatile matter (%)	Lipid[2] (%)	Fatty acid composition[1](%)														
			14:0	15:0	16:0	16:1	17:0	iso 18:0	18:0	18:1	18:2	18:4	20:0	20:1	20:5	22:1	22:5	22:6
Anchovy	—	0.08	8.0	1.0	26.2	7.4	1.3	0.2	7.0	13.9	2.3	1.2	0.7	1.9	9.5	2.4	0.5	13.0
Anchovy (B0308)	2.17	0.28	8.2	1.2	16.7	10.6	1.4	0.6	5.8	18.1	1.8	tr	2.0	0.9	15.4	tr	0.8	14.7
Hake - 8	4.12	0.12	4.1	0.4	17.0	10.2	—	—	4.4	29.2	1.1	—	—	3.3	15.4	—	0.4	11.3
Hake - 9	3.95	0.28	4.4	0.4	18.2	9.6	—	—	5.7	28.2	1.2	—	—	3.9	14.4	—	0.8	10.0
Hake - 10	3.77	0.21	3.3	0.3	21.1	8.5	—	—	4.2	31.5	1.0	—	—	2.7	14.2	—	0.5	10.5
Menhaden (B0204)	2.89	0.30	9.6	1.1	17.9	14.3	2.3	2.4	7.7	16.8	1.8	—	1.8	1.6	12.5	—	1.7	5.5
Herring	—	0.17	5.8	0.6	15.9	4.6	—	0.1	3.4	12.2	1.9	0.2	—	13.2	5.7	24.3	—	8.8

[1]Number of carbon atoms: number of double bonds. Additional fatty acids, tentatively identified but present in amounts of 1% or less, were: 12:0, anteiso 15:0, iso 16:0, 16:2, 18:3, 19:0, iso 20:0, 20:2, 20:3, 21:0, 22:2, 22:3, 22:4, 24:1.
[2]Dry basis

The percentages of volatile matter in the Pacific hake (78-103) samples stored at different temperatures and humidities are shown in Table 2. The moisture content of the different samples was relatively constant during several month's storage in plastic bags at −18°C. The increase in volatile matter after equilibrium had presumably been reached, in the samples stored at 90% relative humidity might indicate gradual changes in the affinity of the FPC samples for water or, possibly, the formation of volatile components other than water.

Gas chromatographic analyses of the methyl esters of the fatty acids from the Pacific hake FPC show that it was relatively stable under most of the storage conditions described (Table 3). Shono and Toyomizu (1972) suggested that the rate of decrease of C22:6 acid could be used as an indication of oxidative deterioration in fish products. There were no apparent decreases in C22:6 acid content at 50% relative humidity. However, at 90% relative humidity, there were very significant decreases of C22:6 acid content of from 8.9 to 26.1% in the temperature range of 21° to 43°C. Thus water activity had more effect than temperature on the stability of this FPC preparation.

Each hake FPC extract described in this paper was separated by silicic acid chromatography into three separate fractions, as previously described (Medwadowski et al., 1971). There were little or no significant changes in the amounts recoverable from each fraction (not shown), and they were not analyzed further.

In general, these observations confirm the relative stability of FPC during storage, even under adverse conditions of temperature and humidity.

Acknowledgments

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TABLE 2.—Changes in the volatile matter of Pacific hake FPC (78-103) with storage at different temperatures and humidities.

Storage time (month)	Average volatile matter (%)						
	Storage conditions[1]:						
	Control	21-50	21-90	32-50	32-90	43-50	43-90
0	5.2						
1	5.4	7.6	10.5	7.8	12.8	7.9	12.5
3	5.2	7.8	10.7	8.1	13.1	8.0	12.4
6	5.3	8.1	11.5	8.7	14.2	7.9	13.4
12	5.8	7.9	12.2	8.3	14.8	7.7	15.4

[1]Hyphens separate degrees Celsius and percent relative humidity.

TABLE 3.—Effect of storage on the lipid composition of Pacific hake FPC (78-103).[1]

Storage conditions[2] T (°C)	RH (%)	Storage time (month)	Total lipid[3] (%)	Percentages of the major fatty acids[4] 14:0	16:0	16:1	18:0	18:1	20:1	20:4	20:5	22:5	22:6	Reduction of C22:6 (%)
		0	0.09	1.3	15.8	3.1	7.5	25.3	3.3	2.9	9.9	1.9	29.1	
		1	0.09	1.4	15.6	3.1	7.4	25.3	3.3	2.8	10.1	1.9	29.2	
−20	AF	3	0.10	1.5	15.9	3.2	7.0	24.9	3.1	2.8	10.2	2.0	29.4	
		6	0.10	2.3	15.1	5.0	6.0	22.8	2.2	2.5	15.1	1.4	27.5	5.5
		12	0.12	2.2	15.4	4.8	6.4	23.7	2.2	2.8	13.7	1.4	27.5	5.5
		1	0.10	1.4	15.6	3.1	7.3	25.4	3.0	2.9	10.3	2.1	28.9	
		3	0.11	1.4	15.6	3.4	8.4	22.8	2.8	3.0	11.1	1.8	29.8	
21	50	6	0.10	1.8	13.7	4.3	7.8	23.2	2.7	3.1	12.9	1.8	28.6	1.7
		12	0.12	2.1	16.2	4.9	6.8	24.2	2.2	2.8	12.9	1.1	26.9	7.6
		1	0.11	1.4	15.4	3.0	7.5	25.1	3.1	2.9	10.2	2.0	29.2	
		3	0.12	1.3	15.2	3.2	9.0	23.7	3.6	2.9	10.2	1.8	29.3	
21	90	6	0.10	1.9	16.8	4.7	7.2	24.1	2.3	2.8	12.3	1.5	26.5	8.9
		12	0.12	2.3	16.1	5.2	6.4	24.1	2.0	3.0	12.9	1.5	26.5	8.9
		1	0.10	1.4	15.9	2.9	7.5	25.3	3.3	2.8	10.6	2.0	28.4	
		3	0.10	1.5	15.4	3.3	8.0	23.5	3.2	2.8	10.6	2.0	29.8	
32	50	6	0.11	1.9	15.2	4.9	8.5	25.1	2.4	2.8	11.5	1.6	26.0	10.7
		12	0.10	2.2	16.7	5.4	5.6	24.4	1.4	2.7	13.9	1.0	26.6	8.6
		1	0.11	1.4	15.5	3.2	7.5	24.3	2.9	2.9	10.1	2.1	30.0	
		3	0.12	1.5	16.3	3.6	8.0	23.5	3.0	3.0	10.5	1.9	28.8	
32	90	6	0.12	1.6	16.4	4.2	8.1	25.3	2.6	2.6	11.2	1.2	26.8	7.9
		12	0.12	2.1	17.6	5.0	7.0	25.8	2.2	2.5	11.4	1.1	25.3	13.1
		1	0.10	1.5	15.2	3.0	8.4	24.7	3.2	3.0	9.6	2.0	29.4	
		3	0.12	1.4	16.5	3.1	8.4	25.2	3.4	2.8	9.3	1.8	28.1	3.4
43	50	6	0.10	1.8	16.6	4.5	7.9	25.6	2.3	2.6	11.5	1.1	26.0	10.7
		12	0.12	2.2	15.6	4.9	6.9	24.4	2.1	2.7	12.9	1.2	27.0	7.2
		1	0.10	1.3	15.5	3.1	8.5	25.9	3.6	3.0	9.0	1.8	28.2	3.1
		3	0.12	1.5	17.0	3.4	8.6	24.9	3.2	2.9	9.1	1.8	27.6	5.2
43	90	6	0.12	2.4	16.7	4.9	7.7	25.3	2.3	2.7	11.3	1.3	25.5	12.4
		12	0.13	3.1	18.8	5.8	7.9	27.9	2.3	2.4	9.7	0.7	21.5	26.1

[1]Values are averages from duplicate or triplicate samples.
[2]T—Temperature, RH—Relative humidity, AF—Ambient freezer humidity.
[3]Based on dry weight of FPC.
[4]Number of carbon atom:number of double bonds. The weight percentages were calculated on the basis of the 10 major acids (shown) constituting 100%.

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LENGTH-WEIGHT RELATIONS FOR FIVE EASTERN TROPICAL ATLANTIC SCOMBRIDS

This paper presents an analysis of fork lengths and body weights of five species of scombrids measured from landings at several ports on the west coast of Africa during 1967 and 1968: yellowfin tuna, *Thunnus albacares*; skipjack tuna, *Katsuwonus pelamis*; bigeye tuna, *T. obesus*; little tunny, *Euthynnus alletteratus*; and frigate mackerel, *Auxis* sp. Sampling of landings took place between 26 September 1967 and 22 May 1968 at the ports of Dakar, Senegal; Freetown, Sierra Leone; Abidjan, Ivory Coast; Tema, Ghana; and Benguela, Angola. Samples were also taken from fish stored at a cannery in Mocamedes, Angola. Fish were captured by bait (pole-and-line) boats, purse seiners, and combinations of both. Only whole fish were used for this study, landed in fresh, iced, frozen, and indeterminate conditions. Fork lengths were usually measured to the nearest centimeter. Weight was usually measured to the nearest 0.1 kg. All nonmetric data were converted to centimeters and kilograms.

The allometric length-weight equation is used to describe the relation between length and weight:

$$W = aL^b e \quad (1)$$

where W = weight in kilograms
L = length in centimeters
a and b = estimated parameters.
e = error term

Results

Estimates of a and b were made for each sample. A wide range in values of a and b occurred for the same species and, in some cases, for the identical sample category (category is defined as port, gear, and method of preservation of fish), that was at first alarming. However, examination of plots of the estimated curves revealed only minor differences among samples at sizes included in the samples. It was also noted that estimates of a are closely related to estimates of b (Figure 1), again indicating the fish at the same length weighed approximately the same.

Analyses of covariance were used to test the statistical significance of differences among length-weight relations within a sample category. F-tests for the significance of differences of the

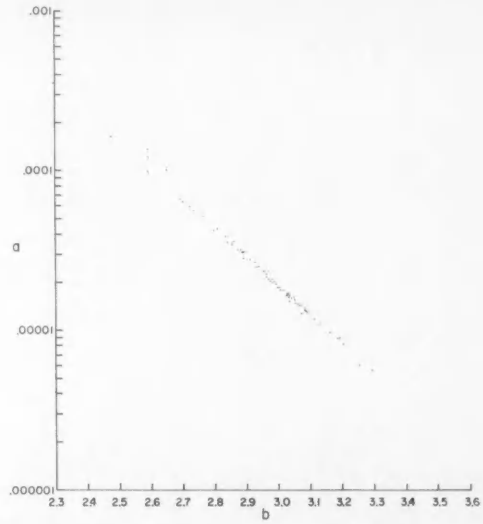

FIGURE 1.—Relation between estimates of a and b of the allometric length-weight relation from samples of Atlantic yellowfin tuna.

estimates of both parameters a and b[1] were made instead of F-tests for each parameter as is usually done, because I believe that the close relation between estimates of a and b demonstrates that no additional useful information would be obtained by making the separate tests. F-values for differences among samples within a category were almost always significant for all species with more than one sample. As mentioned previously, plots of the fitted lines showed only minor differences between samples for sizes found in both samples.

Analyses of covariance were also used to test whether differences among sample categories were present. Nested models were used because the significant differences among lines within sample categories indicated that samples rather than individual fish should be used to estimate the error term of the model. Only data for yellowfin and skipjack tunas were examined because there were insufficient data for the other species. Table 1 presents the analysis of covariance of differences among all sample categories for yellowfin tuna. The F-value for difference among sample categories is statistically significant at the

[1] H_o: $a_i = a_j$ and $b_i = b_j$ where a_i = value of a from ith sample, b_i = value of b from ith sample and $i \neq j$.

TABLE 1.—Analysis of covariance of length-weight relation of yellowfin tuna.

Source	Degrees of freedom	Sum of squares	Mean square	*F*-value
Categories	24	1.321851	0.0550771	3.4115*
Samples within categories	128	2.066484	0.0161444	6.7748*
Residual	3,485	8.304751	0.0023830	
Total	3,637	11.693086		

*Significant at 1% level.

TABLE 2.—Analysis of covariance of length-weight relation of skipjack tuna.

Source	Degrees of freedom	Sum of squares	Mean square	*F*-value
Categories	20	2.560355	0.128018	5.0189*
Sample within categories	84	2.142605	0.0255072	7.3030*
Residuals	2,448	8.550099	0.0034927	
Total	2,552	13.253059		

*Significant at 1% level.

1% level. The *F*-value for difference among samples within a category is greater than that among categories. Table 2 presents results for skipjack tuna. Again the *F*-value is statistically significant at the 1% level, and the *F*-value among samples within categories is greater than that among categories. The reasons for the differences are not known. Although there was considerable overlap of sizes of fish encountered among the samples, size composition of the samples did differ and may have contributed to the differences in the length-weight relations because Equation (1) may not perfectly describe the length-weight relation for fish of all sizes. Figure 2 illustrates the variability found in the length-weight relations of yellowfin tuna. The variability among the relations increases with size as Equation (1) assumes.

Statistics of length-weight relations from combined samples for each species are presented in Table 3.

Discussion

Length-weight relations for yellowfin tuna from the Pacific (Chatwin, 1959), from the Atlantic (Poinsard, 1969), and from the present study are illustrated in Figure 3. There is reasonably close agreement among the three curves at small sizes. The Pacific yellowfin tuna appear to be heavier at larger sizes than fish from the Atlantic, but Chatwin did not include fish larger than 115 cm in his work. Two relations are used in Poinsard's work. A relation between fork length and predorsal length and one between predorsal length and weight. Poinsard tried several functions to explain the relations. In the case of fork length and predorsal length he chose the following function:

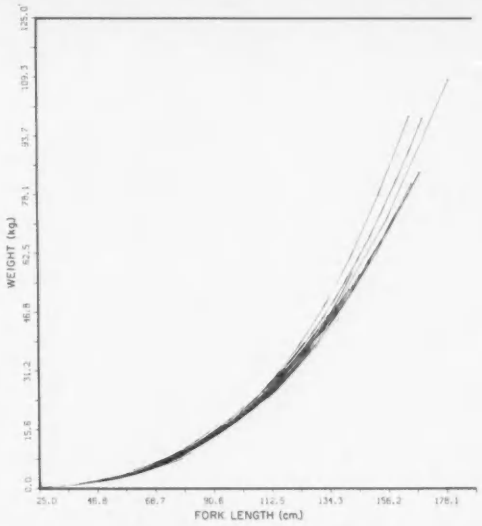

FIGURE 2.—Estimated length-weight relations for all sample categories of Atlantic yellowfin tuna.

$$LD_1 = -16.58774 + 4.66294\sqrt{L} \qquad (2)$$

where LD_1 = predorsal length

He based his choice on the fact that Equation (2) resulted in the highest value of r (correlation coefficient) of the several functions he tried. The value of r when Equation (2) was used was 0.99402, but when a power relation similar to Equation (1) was used the value of r (0.99386) is only slightly less. Figure 3 is based on the square root relation between fork length and predorsal length as recommended by Poinsard. It is very difficult, however, to interpret differences between r values when different dependent variables are used: predorsal length in one case, log (predorsal length) in the other. Equation (2) seems a poor choice because it implies that $LD_1 \leq 0$ when $L \leq 12.65$. The estimated weights using Poinsard's logarithmic relation are illustrated in Figure 4—the two curves are very similar for all lengths. This similarity indicates that the results of Poinsard and of this study are accurate estimates of the average length-weight relationship of eastern tropical Atlantic yellowfin tuna.

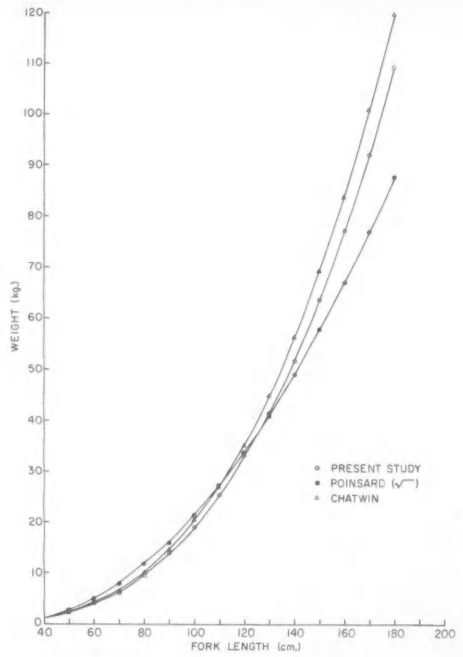

FIGURE 3.—Estimated length-weight relations for yellowfin tuna (Chatwin, 1959; Poinsard, 1969). Poinsard's relation based on square root relation between predorsal and fork length. Chatwin's study did not include fish longer than 115 cm.

Since it is desirable to utilize the function which was estimated directly from either predorsal or fork length data, the results of Poinsard should be used when predorsal lengths are measured and the results of the present study should be used when fork lengths are measured.

Beardsley[2] (pers. commun.) allowed me to examine length and weight measurements of more than 2,000 yellowfin tuna captured in the western Atlantic. These data are very similar to the data used in the present study.

Beardsley and Richards (1970) estimated the parameters of Equation (1) for skipjack tuna and little tunny captured off the coast of Florida. Their estimate of the equation for skipjack tuna is

$$W = 0.00007927L^{3.22750}$$

and for little tunny is

$$W = 0.0000181L^{3.02838}$$

[2]Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, FL 33149.

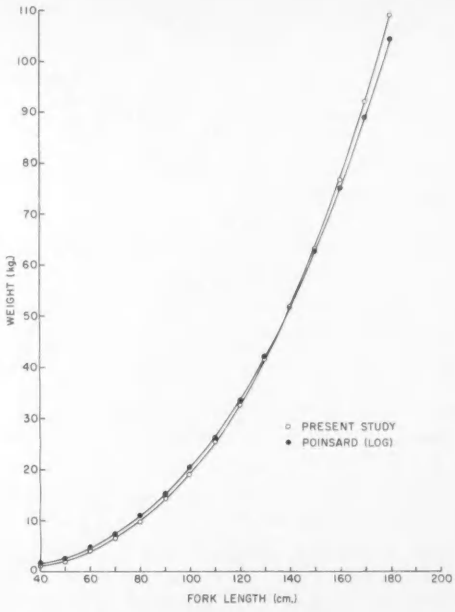

FIGURE 4.—Estimated length-weight relations for yellowfin tuna (Poinsard, 1969). Poinsard's relation based on logarithmic relation between predorsal and fork length.

These results are quite similar to the results of the present study. The range in fork length of skipjack tuna in their study was 38-78 cm and for little tunny 34-87 cm. Since these size ranges exceed the ranges encountered in this study their results should be used. Chatwin (1959) obtained similar results for skipjack tuna from the Pacific, and Batts (1972) for skipjack tuna from the western Atlantic.

The number of frigate mackerel used in this study is too small to produce very meaningful results. The results are presented here only to make them available to other workers.

Several authors including Pienaar and Thomson (1969) have questioned the validity of assumptions made about the error term in Equation (1). Also, the logarithmic transformation results in weight being slightly underestimated even if Equation (1) is correct. Results of simulations by Fox (1973)[3] indicate that b is unbiased and an unbiased estimate of a is given by

$$a' = a \exp\left(\tfrac{1}{2}\,(s^2_{W \cdot L})\right) \qquad (3)$$

[3]Fox, W. W., Jr. 1973. Some simple biologically useful functions and multiplicative error regression models. Unpubl. manuscr. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92037.

TABLE 3.—Statistics of length-weight relations for all data used in study.

Species	Number of fish	a	[1]b	Mean square error	Minimum fork length (cm)	Maximum fork length (cm)
Yellowfin tuna	3,689	0.000021804	2.96989	0.003265	40	170
Skipjack tuna	2,554	0.000005611	3.31497	0.005193	36	64
Bigeye tuna	190	0.000012494	3.12082	0.003405	41	132
Little tunny	753	0.000012000	3.08340	0.006935	41	57
Auxis sp.	50	0.000000280	4.13514	0.030871	30	45

[1]All estimates are significantly different than 0 at the 1% level.

where a' = unbiased estimate of a
$(s^2_{W \cdot L})$ = mean square error about the regression line.

The mean square errors for this study are low (Table 3). Thus the bias should be negligible. The results of this study were examined by comparing average weights of yellowfin used in the study against predicted weights. Differences were negligible as expected.

The significant differences found among samples and categories indicate that the variance of estimated numbers of fish caught, estimated from length frequency samples, could be reduced by a sophisticated sampling scheme which is stratified by category if not sample. Obviously it would be simpler to weigh fish from each sample rather than measure lengths, if one desired to stratify by sample. Logistics rule out this possibility. A formal cost-benefit analysis of the effort required to develop an adequate sampling scheme stratified by category probably would rule out this scheme. The significant differences among samples do point out the desirability of obtaining large numbers of samples rather than large sample sizes in further study of length-weight relations.

Acknowledgments

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ELECTRICAL THRESHOLD RESPONSE OF SOME GULF OF MEXICO FISHES

Threshold voltage is the minimum electrical potential to which an animal responds (Vibert, 1967). Usually threshold measurements are inexpensive and easy to obtain, and they provide guidelines for designing electrical fishing systems. Bary (1956) and Kessler (1965) showed that threshold voltage varied according to water temperature, size of animal, and width of the pulse. Earlier workers clearly demonstrated that threshold voltages are affected by the position of the animal in the electrical field. Klima (1968) documented experimentally the mathematical relationship between the angle of the animal in the

electrical field and its threshold voltage. These authors have defined the basic physical and biological factors which affect the response of selected marine animals to electricity.

To understand more clearly the basic characteristics of electrical fields which control marine fishes, threshold response of selected Gulf of Mexico species was investigated. I determined the minimum threshold voltage (in a field with other specific characteristics) for Atlantic croaker, *Micropogon undulatus*; spot, *Leiostomus xanthurus*; longspine porgy, *Stenotomus caprinus*; chub mackerel, *Scomber japonicus*; and scaled sardine, *Harengula pensacolae*. I further attempted to determine the minimal effective pulse width by estimating the threshold voltage at selected pulse widths.

Procedure

Spot, Atlantic croaker, and longspine porgy were trawled in Mississippi Sound; minimizing injury to fish was accomplished by towing for only 10 min. Chub mackerel and scaled sardines were caught by night-lighting off the Mississippi Coast (Wickham, 1970). The experimental animals were held in shipboard tanks of circulating seawater while being transported to the Laboratory. Only fish acclimated for more than 3 days and in good physical condition were used. Threshold voltages were determined for 140 individuals. Each specimen was subjected to only one test and discarded.

Studies were conducted in a 72 × 45 × 45 cm, 190-liter plexiglass aquarium at temperatures between 15° and 17.5°C; salinities ranged from 19.6 to 26.4‰.

An electrical system providing a uniform electrical field was used. It had a capacitor-discharge stimulation pulse that could be monitored from the center of the aquarium. Pulse shapes which exhibit a rapid rise in amplitude and slow rate of decay, such as capacitor-discharge pulses, are the most effective for controlling fish (Taylor, Cole, and Sigler, 1956; Vibert, 1967; Klima, 1972).

A pulse generator was used for the stimulation pulses. Pulses were applied to two monel electrodes mounted at opposite ends of the aquarium. Pulse characteristics were measured with a pair of pickup probes. These were constructed from two 3-mm diameter bronze rods 10 cm apart and insulated so that only the bottom 10 mm of each rod was exposed. Pulse characteristics were displayed on an oscilloscope as a graph of voltage against time.

Threshold voltages were determined with the fish held immobile parallel to the electric field in a plastic mesh tube in the center of the aquarium facing either the positive or negative electrode. Voltage was slowly increased until the fish responded by fluttering of the body. This value was then recorded from the oscilloscope and assumed to be the threshold voltage.

Results and Discussion

Kessler (1965) found that variations in pulse width alter the threshold voltage for shrimp. Pulse widths longer than 150 μs are satisfactory for stimulating shrimp, whereas below that width the power required for stimulation would be significantly greater. Longspine porgies stimulated with less than 100 μs pulse widths required at least four times more voltage to respond than fish stimulated with a wider pulse (Table 1). At narrow pulse widths threshold voltage was high; at the longer widths it was low, forming an inverse relationship.

Scaled sardine required higher voltages to elicit a response at narrower pulse widths than at wider pulse widths. At 45 μs it took almost 1.9 V/10 cm to elicit a minimum response, but at 100 μs it took only 1.3 V/10 cm, and at 250 and 1,000 μs it took only 1.0 and 0.9 V across 10 cm. A comparison of threshold voltages of scaled sardines at different pulse widths shows a significant difference between the threshold values at pulse widths tested (Table 1). Student's t-test was used in making these comparisons:

$$(t = 6.316, t_{0.975\,(18)} = 2.101) \quad 45 \text{ and } 100\ \mu s,$$

$$(t = 3.815, t_{0.975\,(18)} = 2.101) \quad 100 \text{ and } 250\ \mu s,$$

$$(t = 5.000, t_{0.975\,(18)} = 2.101) \quad 250 \text{ and } 1{,}000\ \mu s.$$

Although there was a difference in the minimum voltage within the 250 μs to 1.0 ms range, as shown by the reactions of scaled sardine, the difference in actual voltage was minimal. For scaled sardine the most efficient pulse width in terms of electrical power would be not less than 250 μs. Generally, threshold voltages at pulse

TABLE 1.—A summay of threshold voltages.

Species	Average V/10 cm	Variance	Pulse width (ms)	Electrode which fish faces	Sample size	Range fish length (mm)
Atlantic croaker	0.39	0.006	2.500	+	10	130-150
Atlantic croaker	0.30	0.001	2.500	−	10	120-150
Spot	0.38	0.048	2.300	+	10	102-132
Chub mackerel	0.31	0.005	2.300	+	15	175-189
Longspine porgy	2.90	0.004	0.045	+	10	90-106
Longspine porgy	1.82	0.004	0.100	+	10	91-106
Longspine porgy	0.35	0.001	0.250	+	10	93-111
Longspine porgy	0.35	0.001	2.500	+	10	92-110
Scaled sardines	1.89	0.331	0.045	+	10	85-98
Scaled sardines	1.00	0.010	0.045	−	5	78-93
Scaled sardines	1.29	0.056	0.100	+	10	80-101
Scaled sardines	0.83	0.003	0.100	−	5	84-91
Scaled sardines	1.00	0.020	0.250	+	10	79-94
Scaled sardines	0.80	0.300	0.250	−	5	88-98
Scaled sardines	0.90	0.020	1.000	+	10	80-99

widths greater than 2,000 μs were similar between species.

Atlantic croaker were used to test the hypothesis that fish require more voltage to show a threshold reaction when facing the positive electrode. Analysis of the average threshold voltages of croakers facing the positive and negative electrode by Student's t-test shows a significant difference between the values

$$(t = 3.60 \text{ and } t_{0.975\,(18)} = 2.101).$$

Scaled sardines showed a similar response (Table 1). These results confirm those of Bary (1956) where he showed that mullet required more voltage to respond when facing the anode than the cathode.

The cost of producing a useful electrical field in seawater is dependent upon the power required to elicit specific responses in the desired species. Pulse width obviously is a major factor which affects the power requirements along with voltage and pulse rate (Klima, 1972). Narrow pulse widths require proportionately less power than wider ones. Engineering design criteria for pulse generators are usually based on the minimum pulse width electronically possible. These results, however, indicate that pulse width should not be less than 250 μs and probably should range between 250 and 1,000 μs.

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OCCURRENCE OF A RATFISH IN THE COLUMBIA RIVER ESTUARY

A ratfish, *Hydrolagus colliei* (Lay and Bennett), was captured in the Columbia River estuary, near the Oregon shore, on 24 August 1972. Commercial fishermen Howard and Mark Simonsen captured the specimen near buoy 21, approximately 8 km upstream from the mouth of the river. They were fishing for salmon in 8 m of water with a dacron gillnet of 8 ⅝-inch mesh and an effective fishing depth of between 10 and 12 m. The fish was caught at 2030 h during an incoming tide; the actual depth, temperature, and salinity at place of capture are unknown. At the time of capture, however, our monitoring station, 3.2 km farther upstream, indicated a water temperature of 13.4°C and a salinity of 5‰ at a depth of 10 m. The salinity was increasing and reached 31‰ 5 h later. The ratfish was an adult male, 445 mm in length, weighing 460 gm (Figure 1). There are no known methods of determining the ages of chimaeroids, including the ratfish (Simmons and Laurie, 1972). The specimen was preserved and is now part of the collection at the facility of the Northwest Fisheries Center, National Marine Fisheries Service, at Hammond, Oreg. Although ratfish are distributed along the coast of western North America from southeastern Alaska to Baja California, including the upper Gulf of California (Hart, 1973), this is the first record of one appearing in the Columbia River estuary. In fact, no chimaeroid has been recorded from any estuarine water (Carl L. Hubbs, Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA 92037, pers. commun).

"*Hydrolagus colliei* is the only species of chimaera reported from the west coast of the United States, and, unlike other species in the family, it generally inhabits relatively shallow water." (Halstead, 1970). According to Hart (1973), ratfish are common visitors to shallow Canadian waters but are most abundant at 92 to 275 m in inside waters and at 183 to 366 m in outside waters. He also reports that they are "in deeper water toward the south (as in northern California)". The occurrence in the deeper water toward the south is real and significant, but they may not occur in deeper waters off northern California because that is an area of extremely cold ocean temperatures (Carl L. Hubbs, pers. commun.). Day and Pearcy (1968) captured ratfish off the Oregon coast at depths between 40 and 200 m. Ratfish are weak swimmers, mostly noctural in behavior, but have been seen swimming at the surface in southeastern Alaska and British Columbia waters (Goode and Bean, 1895).

Maximum spawning activity is in late summer and early fall (Sathyaneson, 1966). On 26 June 1957, a large concentration of ratfish became

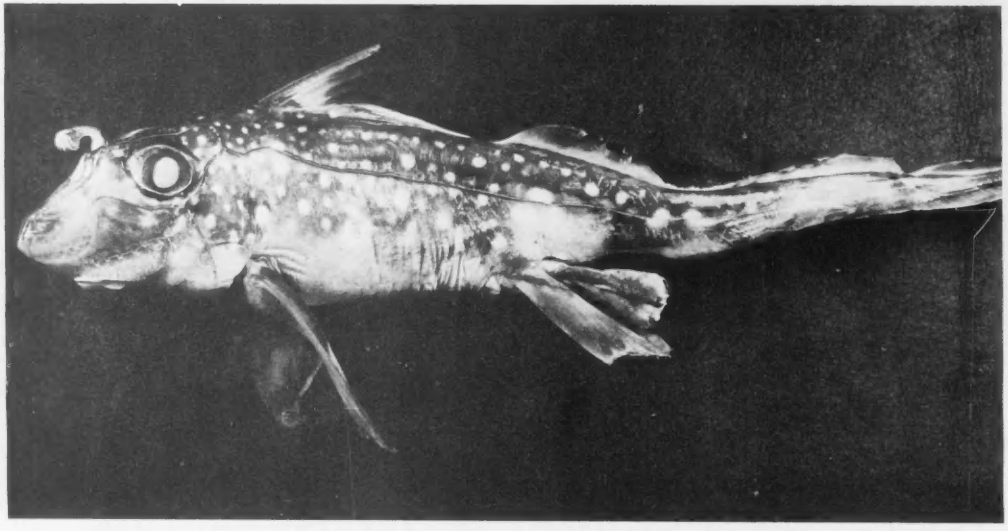

FIGURE 1.—Ratfish, *Hydrolagus colliei*, captured in the Columbia River estuary.

trapped in the tide pools of Cape Arago, Oreg. It was suspected they were spawning near shore (Jopson, 1958).

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UNUSUAL OCCURRENCE OF AN EASTERN BANDED KILLIFISH IN THE LOWER COLUMBIA RIVER

The recorded geographic range for the eastern banded killifish, *Fundulus diaphanus diaphanus*, is in the waters of the Atlantic coastal states from South Carolina north to Newfoundland. They occur in lakes, quiet rivers, and Atlantic coast estuaries (Hubbs and Lagler, 1958).

On 19 August 1971, an eastern banded killifish was collected by the National Marine Fisheries Service on the Oregon side of the Columbia River about 75 km upstream from Astoria. The fish, shown in Figure 1, was taken in shallow water with a 100-m long beach seine. River temperature

FIGURE 1.—Eastern banded killifish, *Fundulus diaphanus diaphanus*, captured in the lower Columbia River.

on the date of capture was 19°C. The specimen was 59 mm in standard length, and coloration was similar to that described by Trautman (1957) for the species, olivaceous on the dorsal surface with a light yellow ventral surface. This specimen also possessed an iridescent blue-green stripe horizontally along each side, which faded rapidly after capture. It is now in the collection of the National Marine Fisheries Service Biological Field Station at Hammond, Oreg. Additional specimens have not been taken in the area, and the authors conclude that the presence of the fish was probably due to an unauthorized release.

The authors wish to thank Carl E. Bond, Oregon State University, Corvallis, Oreg. and Carl L. Hubbs, University of California, La Jolla, Calif. for verifying the identification of the killifish and their review of the manuscript.

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IN MEMORIAM: ROBERT LOUIS DRYFOOS, 1939-1974

A modest and understanding man, an unselfish and loving husband, an affectionate father, a devoted son and grandson, and a dedicated and accomplished scientist, this is a rich life of accomplishment, Robert Louis Dryfoos.

He was always willing to lend a hand to his many friends and colleagues, always dependable in responsibilities, and solid in his accomplishments. He could achieve, whether it meant leading a local centennial parade high up on a Rotarian float as an old New England sea captain, or elucidating the complexities of the migrations of a million fish from Cape Cod to the Gulf of Mexico. His quiet nature belied his status as a respected fisheries expert and research administrator. As an authority on the dynamics of fish populations he made significant contributions to a better understanding of the complex fisheries in the northeast Pacific, the Atlantic coast, and in his most recent work, the fishery resources of the entire United States.

He had a natural curiosity that led him to the ocean at an early age. As a young boy in San Francisco he was never far from the sea, the fresh wet-smell of the surf, the screeching gulls, and the small fishing boats plying their catches under the Golden Gate. His curiosity and his willingness and ability to help others was to be satisfied in a decade of productive fisheries research. Not esoteric problem solving for problem sake, but rather a dedication to learn about the sea and unravel its vagaries of protein production. He collected, sifted, and synthesized previously unknown bits of information, pieced them together meticulously, systematically, and with keen intelligence and patience he would tell us more about how to develop and maintain our fragile fisheries. He teamed with other young and dedicated men, in Seattle, in Beaufort, at Charleston, Woods Hole, La Jolla, Narragansett, and in Washington. He was intent on learning how to better define and manage the wild populations in their tempest environment. And this was a pressing national need, not headline stuff, but the necessary and critical steps to be taken for the fisheries, that all too often are abused, overexploited, and in some cases damaged beyond repair. He chose this direction. He worked. He sweated. He persevered, and he accomplished.

His earliest work was done as a young college undergraduate with the International Halibut Commission in Seattle. He spent months at a time in the north Pacific, rubbing shoulders with halibut fishermen on the banks. They ran their trawls from Seattle up to Sitka in the Aleutians and into the Bering Sea. Bob's affinity to help and make a significant contribution was evident in his interest in going to sea with all the discomforts of tossing ship, hip boots deep in gurry, fish filled checkers, and cold night watches. He learned first hand about fishermen, their problems, the declining stocks, and pondered on how best to rebuild their catches. This early work began a decade of scientific output. While an undergraduate at the University of Washington in 1960 he published his first paper on new range extensions of fish in the north Pacific. His next contribution was made during his graduate

studies, while working part-time and summers for the College of Fisheries at the University. He and his professor reported on their discovery of the egg maturation, embryo development, and birth rates of the ocean perch of the northeast Pacific.

It was at the University of Washington, as an undergraduate that he caught the eye of his senior colleagues as a "comer." They saw in Bob, that all-too-rare combination of an individual with the ability to detect a problem, the desire to get the job done, and the mental prowess to have it done correctly. He was one of the few selected as a Bureau of Commercial Fisheries Fellow, and worked under this fellowship grant from 1962 to 1964, earning his doctorate in fisheries in 1965 from the University of Washington. His doctoral thesis is an important contribution on the life history and ecology of populations of smelt in Lake Washington. This study of the smelt and associated limnetic species in Lake Washington also has provided a data base for future examinations of changes in the fauna. The study was conducted at a peak of eutrophication in Lake Washington. Public concern, aroused in 1956, culminated in the creation of the Municipality of Metropolitan Seattle (Metro) in 1958 which was charged to develop an effective sewage-disposal system for the entire area. The Metro Program, at a total cost of about $121 million, began diverting sewage from the lake in 1963 and was completed in 1968. In 1968 experts described Lake Washington as a classic case history study of eutrophication and recovery. Changes in the lake's fish populations since this study of the smelt have been marked and are the subject of more recent studies at the College of Fisheries, University of Washington.

The young scientist then moved from Seattle to Beaufort, N. C., to take up the challenge of Government efforts to assist in the revitalization of an ailing menhaden industry. Under his supervision, an ambitious and successful program was undertaken to solve the mystery of menhaden migrations. His team tagged an unprecedented number of fish, some one million, from Long Island to Florida. They proved conclusively that menhaden move north in spring and summer and south in fall. Vital information on fishing mortality and natural mortality was obtained for this resource. His menhaden work for the 7 yr from 1965 to 1971 laid the foundation for what is to become the model program for State-Federal partnership in managing our domestic fisheries. During early 1974 in Washington, an historic meeting took place where his former colleagues presented the first comprehensive plan for managing this valuable but overexploited resource, worth some $50 million a year to the economy. This plan could not have been prepared without the inspired and dedicated work of Bob Dryfoos.

With his menhaden work completed, Bob moved on to greater responsibility at Narragansett, R. I. He was instrumental in developing the first comprehensive national program for assessing the important living resources of our coastal and continental shelf waters. The new initiative is called MARMAP for the Marine Resources Monitoring, Assessment, and Prediction Program. In his April 1972 budget message to Congress, the President cited this program as one of the more significant contributions to our civilian oceanographic effort. MARMAP was another "first" for Bob Dryfoos. He helped shape the concept, and mold the national fiber. Like other new initiatives it was subjected to criticism and doubt. But Bob believed in the concept, and with his colleagues he persevered. Nationally coordinated assessments of fishery resources are now being made from the Gulf of Maine to the Caribbean, the Florida Keys to the Bay of Campeche, from Baja California to the east Bering Sea and in the oceanic waters of the tropical Atlantic and Pacific. The results of his MARMAP efforts are just now bearing fruit, and will continue to yield more important results in the latter half of this decade, in the 1980's and beyond.

Bob will be missed by his many friends and colleagues. His accomplishments were considerable. A fine heritage for his dedicated wife Carol, son Ricky, daughter Janet, and his parents. He always found time in a busy schedule for civic activities, Rotary, the kids' skating, Cub Scouts, swimming, and clamming, and all those wonderful pursuits that bring enrichment to a family and their friends, and their community. He leaves behind many wonderful memories. We are all richer from our association with him.

His outstanding record remains with us, and from his contributions we will move on, we will keep building, for a better and rational and more enlightened tomorrow.

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ERRATA

Fishery Bulletin, Vol. 72, No. 1

WAHLE, ROY J., ROBERT R. VREELAND, AND ROBERT H. LANDER, "Bioeconomic contribution of Columbia River hatchery coho salmon, 1965 and 1966 broods, to the Pacific salmon fisheries," p. 139-169.

The captions of the Appendix Tables on pages 162-165 are correct, but the tabular entries below were transposed:

1) Tabular material on page 165 should have appeared on page 162;
2) Tabular material on page 162 should have appeared on page 163;
3) Tabular material on page 163 should have appeared on page 165.

Fishery Bulletin, Vol. 72, No. 2

APRIETO, VIRGINIA L., "Early development of five carangid fishes of the Gulf of Mexico and the south Atlantic coast of the United States," p. 415-443.

1) Page 419, left column, lines 13 and 14 should read: hemal spine of the first caudal vertebra. In adults, these spines are only slightly differentiated from

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Manuscripts submitted to the *Fishery Bulletin* will reach print faster if they conform to the following instructions. These are not absolute requirements, of course, but desiderata.

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The **title page** should give only the title of the paper, the author's name, his affiliation, and mailing address, including Zip code.

The **abstract** should not exceed one double-spaced page.

In the **text**, *Fishery Bulletin* style, for the most part, follows that of the *Style Manual for Biological Journals*. Fish names follow the style of the American Fisheries Society Special Publication No. 6, *A List of Common and Scientific Names of Fishes from the United States and Canada*, Third Edition, 1970. The *Merriam-Webster Third New International Dictionary* is used as the authority for correct spelling and word division.

Text footnotes should be typed separately from the text.

Figures and **tables,** with their legends and headings, should be self-explanatory, not requiring reference to the text. Their placement should be indicated in the right-hand margin of the manuscript.

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Acknowledgments, if included, are placed at the end of the text.

Literature is cited in the text as: Lynn and Reid (1968) or (Lynn and Reid 1968). All papers referred to in the text should be listed alphabetically by the senior author's surname under the heading "Literature Cited." Only the author's surname and initials are required in the **literature cited.** The accuracy of the **literature cited** is the responsibility of the author. Abbreviations of names of periodicals and serials should conform to *Biological Abstracts List of Serials with Title Abbreviations. (Chemical Abstracts* also uses this system, which was developed by the American Standards Association.)

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Fifty **separates** will be supplied to an author free of charge and 100 supplied to his organization. No covers will be supplied.

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